

IN THIS ISSUE

The genus *Botrychium* has been the subject of an enormous amount of research in recent decades, including the discovery of numerous new species, especially in the northern United States and Canada. Because of the diminutive size, these plants are easily overlooked. The first article is an illustration of this. It is a report of a systematic search in an area of extreme northwestern Minnesota which saw the increase in the number of collections in that area from nine in 2005 to 666 by 2020, representing 12 species.

Pitcher's Thistle (*Cirsium pitcheri*) is one of the best known rare and endangered species in the upper Great Lakes area and as a result has received much attention from ecologists. One such study is presented in the second article, which examines how local, small-scale environmental factors on Beaver Island in Lake Michigan affect the local distribution of individuals within a habitat and describes how these findings have implications for reintroduction and management practices involving endangered species, especially in the face of climate change.

The third article is part of a continuing series of studies of the Grand Rapids area flora and how it has changed since Emma Cole's 1901 *Grand Rapids Flora*. In this article, the authors assess nine high-quality wooded sites within an undeveloped area that is scheduled to be designated as a future Kent County park, the Lowell Regional Greenspace. Botanical inventories of these nine sites revealed that eight of them are floristically significant on a statewide basis and that there were remarkable differences in floristic composition even between sites classified as the same community type. This indicates the importance of preserving remnant habitats, even those of a small size.

Molecular data is particularly useful in assessing the phylogenetic relationships among species. In the fourth article, this technique is applied to North American species of hazelnut (*Corylus*). The authors confirm that the two eastern species, *C. americana* and *C. cornuta*, are derived from separately evolving lineages, but nevertheless are more closely related to each other than either is to other species in the genus based on DNA sequences from chloroplast genomes, which is hypothesized to be the result of hybridization or introgression. *Corylus californica*, in western North America, which had previously been treated as a subspecies or variety of *C. cornuta*, is shown to best treated as a separate species that separated from *C. cornuta* before the introgression of the two eastern species.

This issue concludes with the first report for Michigan of the invasive mile-a-minute weed, *Persicaria perfoliata*, and two book reviews—a review of an excellent new identification manual for the trees, shrubs, and woody vines of Arkansas and a review of a second outstanding manual covering the sedges of Indiana, this one covering the giant genus *Carex* (the previous volume had covered the other 18 Indiana genera of sedges).

—Michael Huft

DISTRIBUTIONS OF SPECIES OF *BOTRYCHIUM* (OPHIOGLOSSACEAE) IN NORTH-NORTHWESTERN MINNESOTA

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ABSTRACT

From 2005 to 2020, we conducted targeted field surveys in northwestern Minnesota across those portions of Koochiching, Lake of the Woods, Roseau, Beltrami, Marshall, Polk, Pennington, and Kittson Counties that lie north of the 48th parallel for any of the fifteen species of *Botrychium* known to occur in Minnesota. Prior to 2005, there were only nine populations of *Botrychium* recorded from this area. During our 16-year survey, we took 640 collections. Vouchers were accessioned at the University of Minnesota Bell Museum Herbarium. Data were reported annually to the Minnesota Department of Natural Resources and entered into the Natural Heritage Information System database. All collections in this database from this area are accounted for in this report, 666 in total. Twelve taxa are represented, some of them common, and others among the rarest species of *Botrychium* in Minnesota. Ten taxa are currently listed in Minnesota as rare, threatened, or endangered; an eleventh likely will be. Distributions are influenced by the landscape history from early post-glacial to present. Changes in vegetation from pre- to post-settlement have been influenced by logging practices, fire suppression, widespread drainage and agricultural conversion, and settlement history. Broad distribution patterns of *Botrychium* in pre-settlement times would likely have been similar to present, but the specific habitats suitable to *Botrychium* on this landscape have changed profoundly with the post-settlement changes in the vegetation. Micro-distributional observations in rich sites suggest a few possible associations that are unusually predictive.

KEYWORDS: *Botrychium* distributions, northwestern Minnesota

INTRODUCTION

The genus *Botrychium* Sw. is one of four genera of the family Ophioglossaceae that occur in Minnesota. The Ophioglossaceae is the sole family in the order Ophioglossales, an early-diverging lineage only distantly related to most other ferns (Lellinger 1985). Like other ferns, *Botrychium* has both a sporophyte generation and a gametophyte generation; both are subterranean except that the sporophyte plant may produce a single leaf per year above ground. This has a distinct morphology, with two parts, separating at or above ground level into a fertile portion, the sporophore, bearing clusters of spherical sporangia, and a sterile portion bearing pairs of leaf-like pinnae. Subtle details of pinna morphology, particularly at the margins, are important for species-level identification. Care is essential in preparation of specimens because the pinnae tend to shrivel on drying unless they are dried under sufficient pressure.

Particularly important to understanding the distribution and ecology of *Botrychium* species is that they have an obligate mycorrhizal associate that provides the plant with water, minerals, and carbohydrates and that may reduce

competition and thereby the need to make other adaptations to partition available habitat resources (Farrar 2011). The presence of genus communities of multiple species with little discernable segregation of habitat is common (Wagner and Wagner 1983) and is likely facilitated by these mycorrhizal associates. The suitability of otherwise potential habitat depends on the presence of mycorrhizal associates, something not directly observable in field surveys.

The genus is mostly circumboreal in distribution and is most diverse in North America. Consequently, *Botrychium* species are largely associated with previously glaciated habitats and reach lower latitudes at higher elevation sites. Nine diploid species are known from Minnesota and six allotetraploids (Farrar 2011). Most collections are from the northern third of the state.

We have found north-northwestern Minnesota to be particularly rich in *Botrychium* species, in both diversity and abundance. This is especially true of large contiguous areas of public land within the Beltrami Island State Forest and the Red Lake Wildlife Management Area and in limited portions of Pine Island State Forest to the east. The pre- and post-settlement landscape history that is somewhat unique is largely responsible for the sustained presence of these species in this part of the landscape.

Our survey area (the “Survey Area”) extends from the eastern border of Koochiching County in north-central Minnesota to the North Dakota border on the west, and from 48 degrees north latitude to the Canadian border. This is an area approximately 296 by 119 kilometers. Over 95 percent of all collections within this area are our own, and we have visited the sites, examined specimens, or both for all other collections. Only nine populations of *Botrychium* were recorded from this area prior to 2005.

Collection History

The earliest *Botrychium* collection in the Survey Area was from Garden Island in Lake of the Woods in 1894. This site was collected twice in July. Specimens were initially identified as *Botrychium lunaria*, but were later determined to be a mixed collection of *B. neolunaria* and *B. minganense*. No further collections were recorded until 1978, when *B. minganense* was collected from Beltrami Island State Forest in eastern Lake of the Woods County. *Botrychium gallicomontanum* was first collected south of the Survey Area in Norman County in 1988 (Johnson-Groh 1986, MIN 794762[1305608]). Searches for additional populations in native prairies of Marshall and Kittson Counties followed in 1997 and 1998. These efforts did result in the discovery of one additional population of *B. gallicomontanum* in central Kittson County, where it occurs with *B. simplex* and *B. campestre* var. *campestre*. Four other *Botrychium* populations were discovered in Marshall and Kittson Counties during these searches in 1997. Data for the nine populations collected before 2005 are listed in Table 1.

There were no further collections until we began work in Koochiching County in 2005. Twelve collections of four species were made by staff of the Minnesota Biological Survey between 2010 and 2012. Six collections of four species were made by environmental contractors. There were also thirteen sight records without voucher, including six species, from various sources. The re-

TABLE 1. Collection data for the nine *Botrychium* populations from the Survey Area recorded before 2005. All of these collections are at the University of Minnesota Bell Museum Herbarium (MIN). Collection sites are Garden Island, Lake of the Woods (GI), Beltrami Island State Forest (BISF), Lake Bronson State Park (LBSP), Skull Lake Wildlife Management Area (SL), and Middle River (MR).

Species	Site	Date	Collector and Number	MIN Accession Number
<i>B. neolunaria</i>	GI	Jul 31, 1894	MacMillan 2631	50124[1312197]
<i>B. minganense</i>	GI	Jul 31, 1894	MacMillan 2631	754180[1312599]
<i>B. minganense</i>	BISF	Jul 11, 1979	Boe 721	772660[1312620]
<i>B. gallicomontanum</i>	LBSP	Jun 5, 1997	Johnson-Groh 2126	429973[1305606]
<i>B. simplex</i>	LBSP	Jun 5, 1997	Johnson-Groh 2125	460116[1314582]
<i>B. simplex</i>	SL	Jun 6, 1997	Johnson-Groh 2120	429979[1314617]
<i>B. matricariifolium</i>	SL	Jun 6, 1997	Johnson-Groh 2121	460107[1312389]
<i>B. campestre</i>	MR	Jun 5, 1997	Johnson-Groh 2122	430076[1309836]
<i>B. simplex</i>	MR	Jun 5, 1997	Johnson-Groh 2123	460181[1314484]

mainder are our own, 640 in all, between 2005 and 2020. This area is north of the mixed northern hardwoods of Chippewa National Forest, which is the center of greatest concentration of *Botrychium mormo* W. H. Wagner. Between them are the broad patterned peatlands north of Red Lakes. This area was chosen for the potential of suitable habitat and the scarcity of previous collections or search efforts.

Twelve of Minnesota’s fifteen *Botrychium* species are now known to occur here, including all but one of the rarest species in Minnesota. To date, *B. mormo*, *B. angustisegmentum* (Pease and Moore) Fern., and *B. crenulatum* W. H. Wagner, have not been found here. The latter has been collected from only one site in Minnesota, in Chippewa National Forest in Itasca County. We made collections in Lake of the Woods and Roseau Counties in June of 2021 that are most likely *B. crenulatum* (Farrar, personal communication), but genetic confirmation is still pending. The other two species have been well collected from Chippewa National Forest and surrounding parts of Itasca, Cass, and Beltrami Counties due to concentrated search efforts by the Minnesota Biological Survey in the 1990s for populations of the then recently described *B. mormo*. These species may be marginally out of their optimum range in the Survey Area, which lacks the concentration of quality mature northern hardwood habitats.

Landscape History

The Survey Area was once inundated by glacial Lake Agassiz. On the east, most of the area falls within the Agassiz Lowlands subsection of the Laurentian Mixed Forest Province (the natural communities referred to here are described in Minnesota Department of Natural Resources 2003), a relatively flat and poorly drained landscape supporting some of the most significant peatlands in the world. On the west, from central Roseau and eastern Marshall Counties, it transitions into the Tallgrass Aspen Parklands Province, a mosaic of tallgrass prairie, prairie wetlands, groves of *Populus tremuloides* Michx., and scattered *Quercus*

macrocarpa Michx., and finally to Prairie Parkland approaching the Red River (Minnesota Department of Natural Resources 2005).

The peatland landscape is crossed by a succession of beach ridges that mark various stages in the recession of glacial Lake Agassiz (Eng 1979). These are the habitats most suitable to *Botrychium* species, both pre- and post-settlement. Pre-settlement vegetation was predominantly *Pinus banksiana* Lamb. (Jack pine) in open-canopied woodlands or savannas with an open understory; small openings or meadows occurred throughout (Heinselman 1974). On the east, into Koochiching County, beach ridge vegetation transitioned to boreal conifer-hardwood forest. Pre-settlement vegetation is mapped by Marschner (1974), compiled from U.S. General Land Office survey notes.

This part of the state was not open to settlement until 1889, and public land surveys were ongoing from 1895 through 1907. Extensive ditching projects were underway by 1910 in an attempt to drain vast swamplands for agriculture. Logging was on the decline already by the 1920s, and most of the landscape soon proved to be poorly suited to agriculture. By 1929, the state began taking title to tax-delinquent properties, particularly in Lake of the Woods, Beltrami, and Koochiching Counties. By 1936, under the Beltrami Island Land Utilization Project, the Resettlement Administration started to buy out and relocate willing settlers, because county tax revenues were insufficient to provide necessary services in these remote areas (North 2013). This ultimately put large contiguous tracts of land under state administration, much of it now in Beltrami Island State Forest and Red Lake Wildlife Management Area. Meanwhile, logging and post-settlement fire suppression substantially altered the vegetation on the beach ridges where most of the settlement had occurred. Abandoned homesteads, old fields, and other remnants of settlement now comprise the major openings in the landscape.

Many of these sites have remained relatively open for up to eighty years with minimum further disruption and are now the primary refugia for species of *Botrychium* remaining on this landscape. These range from narrow roadsides of forest roads and logging trails or old log landings to borrow pits, old-fields, homesteads, post office, church, school or town sites, logging camps, CCC camps, and airfields, to list a few.

MATERIALS AND METHODS

Survey sites were chosen subjectively, based on an intuitive judgment of potential suitability. Some openings were initially selected by examination of aerial photographs, but all final decisions were made on the spot in the field. In the east, forest roads tend to follow the old Lake Agassiz beach ridges between large basins of peatlands. To the west, drainage efforts were more successful; much of that area is now cultivated, and more marginal tracts are grazed. Searchable public lands there are more limited, and most are large prairie wetlands, but there are some remnants of dry to mesic oak savanna.

Searches were qualitative ground surveys, conducted on foot or on hands and knees. Collections were made at every *Botrychium* occurrence site. These were pressed and sent to the University of Minnesota, Bell Museum Herbarium (MIN). Collection data were reported annually to the Minnesota Department of Natural Resources and were entered into the Natural Heritage Information System (NHIS) database (Minnesota Department of Natural Resources 2021), which provides information on Minnesota's rare plants, animals, and native plant communities. The NHIS database includes

all vouchered collections of state listed or tracked species, historical to present, so it provides an inclusive source of information for verifiable *Botrychium* distributions in the Survey Area current through 2020. All collections in the NHIS database from this area are included in this summary. Although twenty-six collections were not our own, they were likely collected in the same manner.

Many of our pressed specimens were photographed, and the images were reviewed by Don Farrar at Iowa State University for confirmation of identifications. When there were lingering uncertainties, additional collections were made and fresh specimens sent for genetic confirmation by enzyme electrophoresis.

Routine collections took the above-ground leaf only, cut at ground level, leaving the viable plant in place and unharmed. This leaf has all the morphological features required for a reliable identification and verification if proper care is taken to prepare and press the specimen so that features of the pinnae margins are fully visible. Even so, the morphology of some species can be variable enough that a final determination may require genetic verification. Some collections may take a sizable part of the observed population so that some assessment of morphological variation within the population can be evaluated. This can be critical because atypical individuals, considered alone, can lead to misidentifications.

Our evaluation of the suitability of some microhabitats evolved over the period of our surveys. For this reason, some sites were revisited, sometimes more than once, and often yielded additional species in microhabitats previously overlooked.

All 666 collections from the Survey Area from 1984 to 2020 were tabulated. The collection data are accessible in a searchable interface at the Minnesota Biodiversity Atlas (University of Minnesota, Bell Museum 2021). There are also 13 sight records, which were not included in the tabulation because they are not verifiable, but they are maintained in the NHIS database. Maps were generated from the tabulated data. Each dot on the maps represents one collection. An estimated fifteen populations were re-collected for more mature specimens, or for fresh specimens for genetic testing.

Collection frequencies were tabulated by species for an overview of *Botrychium* community composition on this landscape. Distributions were mapped for each species for overall patterns and variability by species. Qualitative observations of habitat characteristics for each collection helped to evaluate where suitable *Botrychium* refugia may be anticipated on this post-settlement, post-fire suppression landscape. Micro-habitat observations have helped to anticipate where, in a given site with a diverse genus community, certain species may be clustered.

RESULTS

Table 2 summarizes all *Botrychium* species collected in the Survey Area through 2020. *Botrychium simplex* var. *simplex* accounts for 30 percent of all collections, followed by *B. pallidum* at 21 percent. This is roughly consistent with state-wide statistics for these species, due largely to the fact that a majority of *Botrychium* collections are from the northern third of the state. Note that the NHIS database does not yet separate *B. simplex* and *B. tenebrosum* as we have done.

Botrychium matricariifolium, which constitutes 16 percent of the collections, is likely also consistent with state-wide statistics, but the Department of Natural Resources has not tracked that species since 2013. These three species account for 68 percent of the total collections. None of the remaining nine species comprises more than nine percent of the total collections. Three of them are exceedingly rare in Minnesota: *B. gallicomontanum*, *B. spathulatum*, and *B. campestre* var. *lineare*.

Figures 1–12 are distributional maps for each species. Eight of these show a concentration of collections within Beltrami Island State Forest and Red Lake Wildlife Management Area in Lake of the Woods and eastern Roseau Counties.

TABLE 2. Summary of collections from (i) the entire Survey Area and (ii) the area of greatest frequency within Beltrami Island State Forest and Red Lake Wildlife Management Area (AGF). For the latter, the percentage of collections from Habitats 1 (roadsides, trails, log landings, airfields, borrow pits and clear cuts) and from Habitats 2 (homesteads, old-fields, and school, church, post office and town sites, CCC camps and logging camps) are indicated. All collections from the Minnesota NHIS database (Minnesota DNR 2021) are included. State listing status is indicated in parentheses following the species name, as follows: Endangered (E), Threatened (T), Special Concern (SC), and Not Listed (NL).

Species	Collection Area				
	Entire Survey Area		AGF		
	Number of Collections	Percentage of Total	Number of Collections	%age in Habitats 1	%age in Habitats 2
<i>Botrychium simplex</i> E. Hitchcock var. <i>simplex</i> (SC)	202	30	159	58	37
<i>Botrychium pallidum</i> W. H. Wagner (SC)	141	21	117	34	64
<i>Botrychium matricariifolium</i> (Döll) A. Braun (NL)	108	16	89	33	66
<i>Botrychium minganense</i> Victorin (SC)	56	8	36	19	78
<i>Botrychium michiganense</i> A. V. Gilman, Farrar & Zika (NL)	39	6	34	21	76
<i>Botrychium neolunaria</i> Stensvold & Farrar (T)	33	5	21	10	90
<i>Botrychium ascendens</i> W. H. Wagner (E)	32	5	24	25	75
<i>Botrychium tenebrosum</i> A. A. Eaton (SC)	32	5	30	47	50
<i>Botrychium campestre</i> W. H. Wagner & Farrar var. <i>campestre</i> (SC)	10	2	4	75	25
<i>Botrychium spathulatum</i> W. H. Wagner (E)	7	1	0		
<i>Botrychium gallicomontanum</i> Farrar & Johnson-Groh (E)	4	0.6	0		
<i>Botrychium campestre</i> var. <i>lineare</i> (W. H. Wagner) Farrar (E)	2	0.3	0		
TOTALS	666		514	39	58

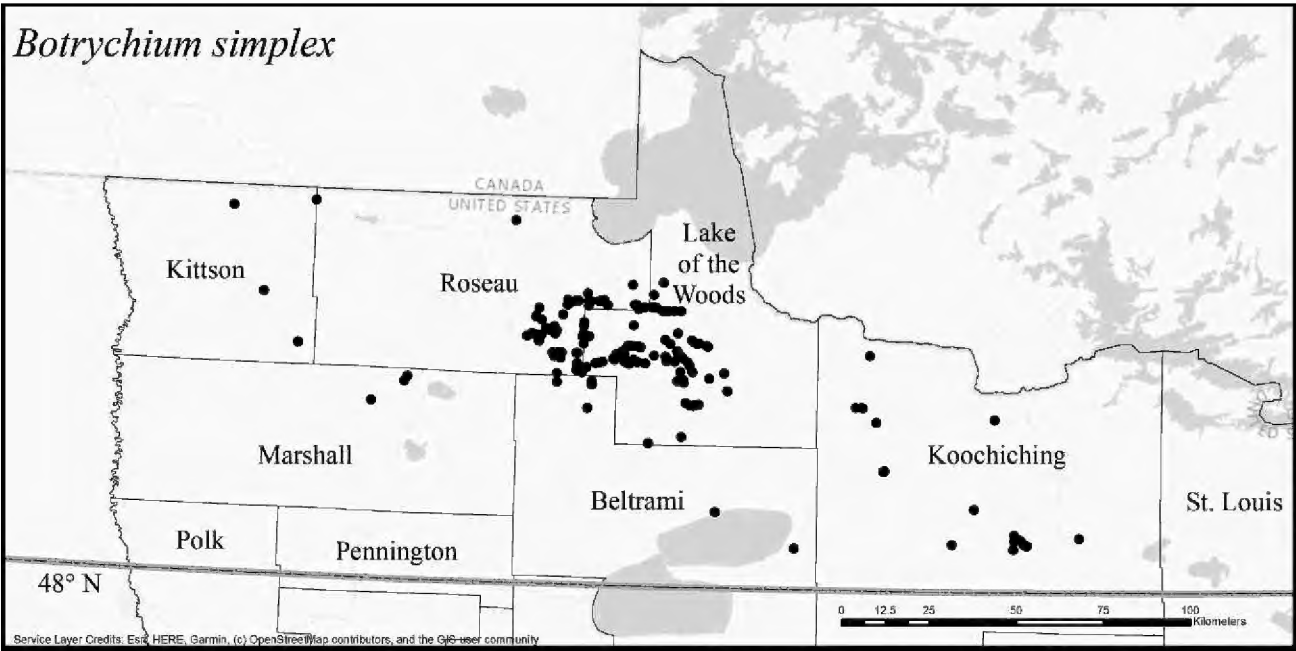


FIGURE 1. Distribution of *Botrychium simplex* var. *simplex* collections in the Survey Area.

Undoubtedly the greater availability of searchable public lands, particularly compared to areas to the west, contributes to this concentration, but other factors are suggested in the Discussion section below. The pattern is most apparent for the most frequently collected species, *Botrychium simplex* var. *simplex* (Figure 1), *B. pallidum* (Figure 2), *B. matricariifolium* (Figure 3), and, to a lesser extent, *B. minganense* (Figure 4), *B. michiganense* (Figure 5), *B. neolunaria* (Figure 6), *B. tenebrosum* (Figure 7), and *B. ascendens* (Figure 8). *Botrychium campestre* var. *campestre* (Figure 9), a prairie species, centers somewhat to the west where there is also a reliable sight record from central Kittson County. The three rarest

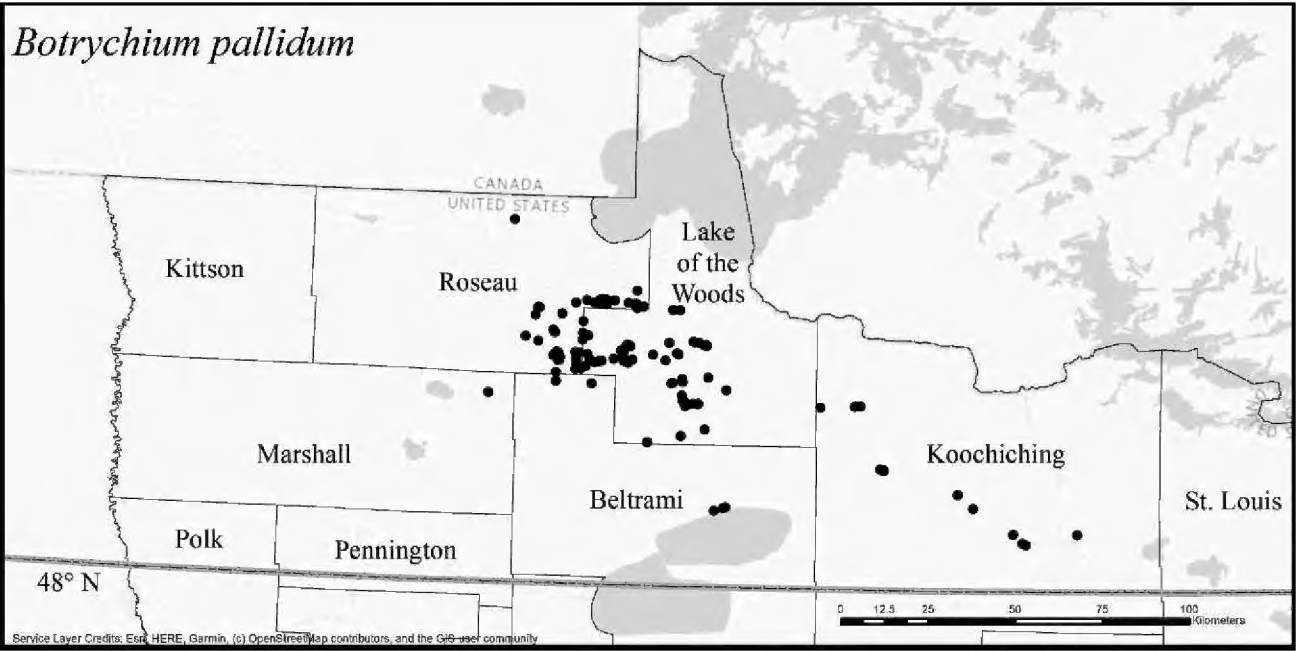


FIGURE 2. Distribution of *Botrychium pallidum* collections the Survey Area.

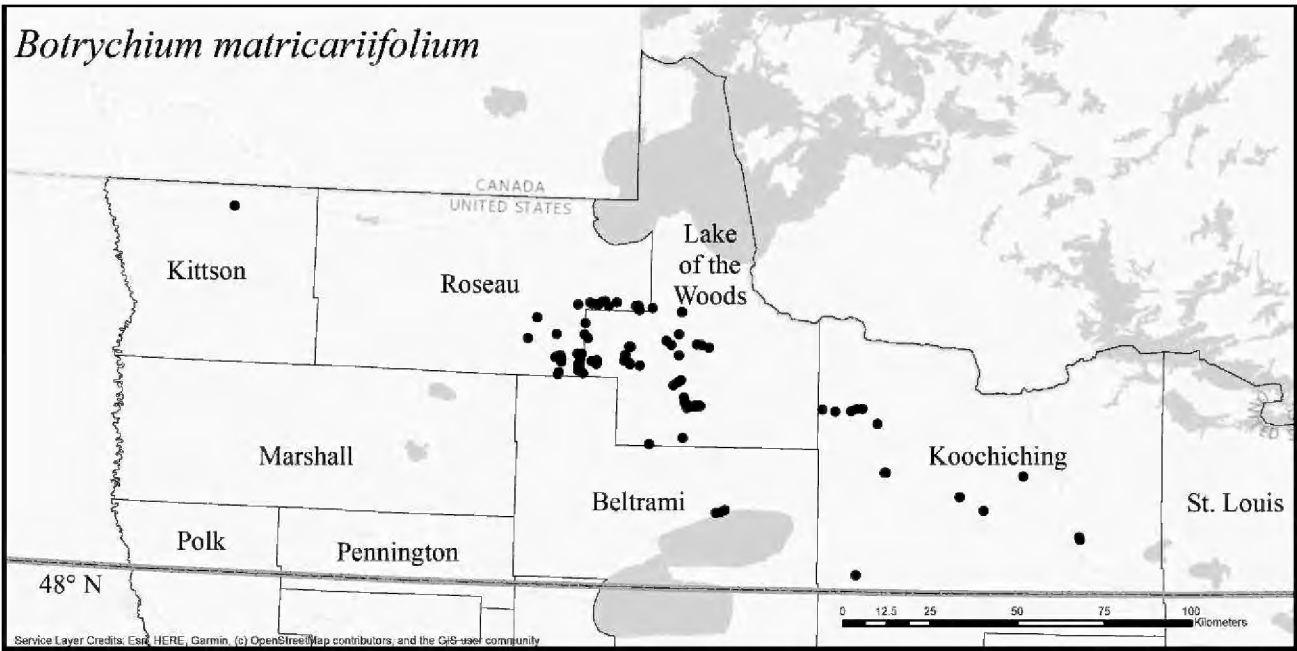


FIGURE 3. Distribution of *Botrychium matricariifolium* collections in the Survey Area.

species, *B. spathulatum* (Figure 10), *B. gallicomontanum* (Figure 11), and *B. campestre* var. *lineare* (Figure 12), have been collected only from the west in Marshall and Kittson Counties.

Within Beltrami Island State Forest and the Red Lake Wildlife Management Area, 97 percent of the collections come from historically disturbed habitats altered by settlement and logging practices. Table 2 includes a summary of habitat data from MacFarlane and MacFarlane (2020) sorted into two major groups: Habitats 1 includes roadsides, trails, log landings, airfields, clear-cuts, borrow pits and powerline corridors; Habitats 2 includes abandoned homesteads, old-fields, logging camps, CCC camps, school, church, post office and town sites.

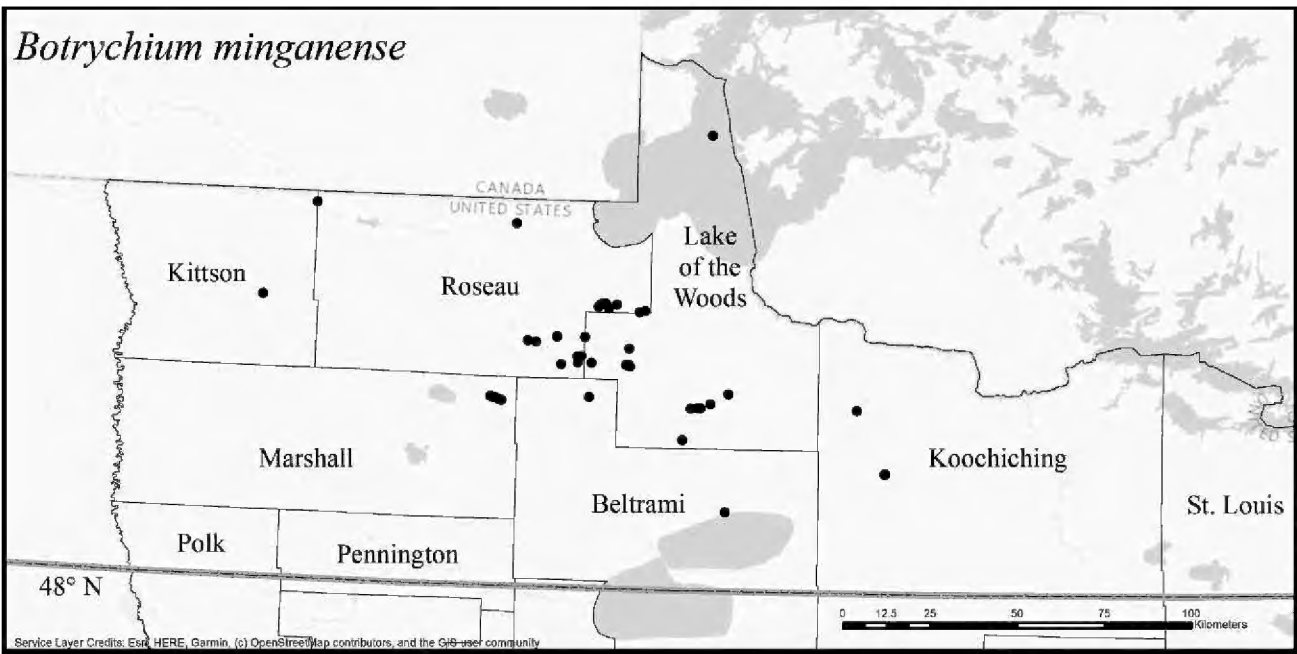


FIGURE 4. Distribution of *Botrychium minganense* collections in the Survey Area.

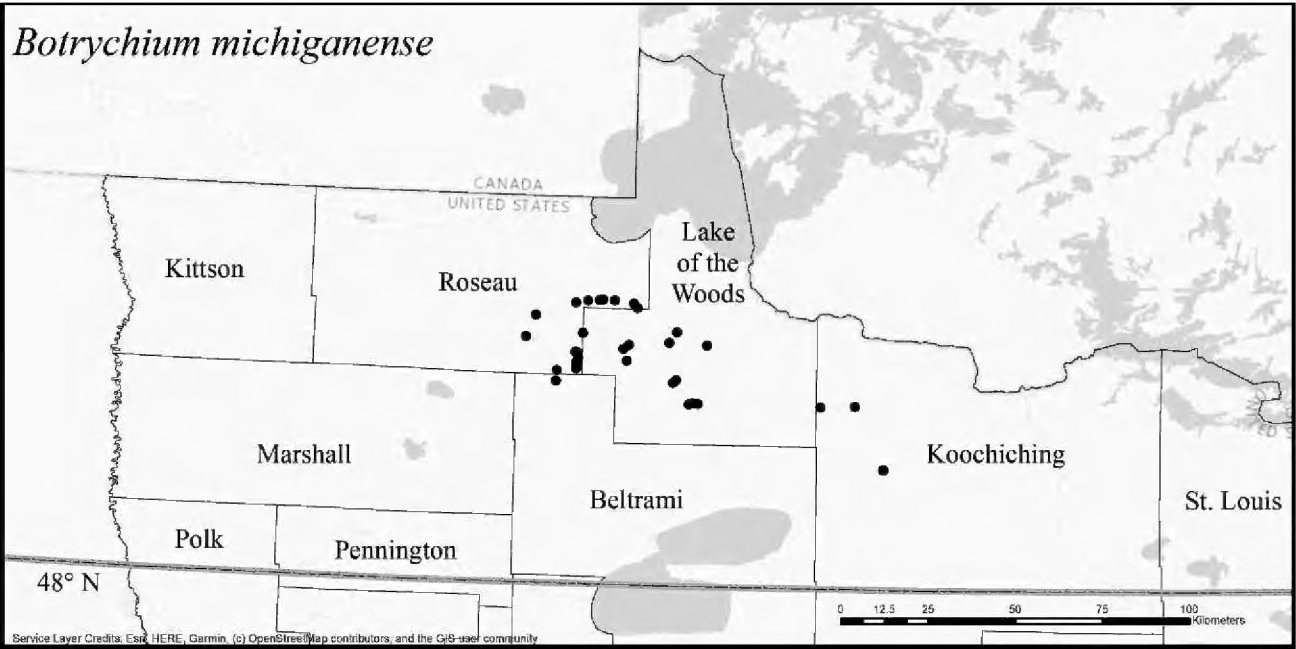


FIGURE 5. Distribution of *Botrychium michiganense* collections in the Survey Area.

The remaining three percent of the collections are largely from second growth *Pinus banksiana*, *Abies balsamea* (L.) Mill. (Balsam fir), pine plantations, and wetland margins.

Most species were more frequent in the Habitats 2 group, which account for 58 percent of all collections. Habitats 1 sites (39 percent of collections) were favored by two species, *Botrychium simplex* var. *simplex*, which was the most frequent species collected from roadsides and trails, clear cuts and log landings, and *B. campestre* var. *campestre* which, for lack of native prairie in this area, favored borrow pits. *Botrychium tenebrosum* was most evenly distributed between them.

Where collections are most frequent, it is apparent that they cluster in corri-

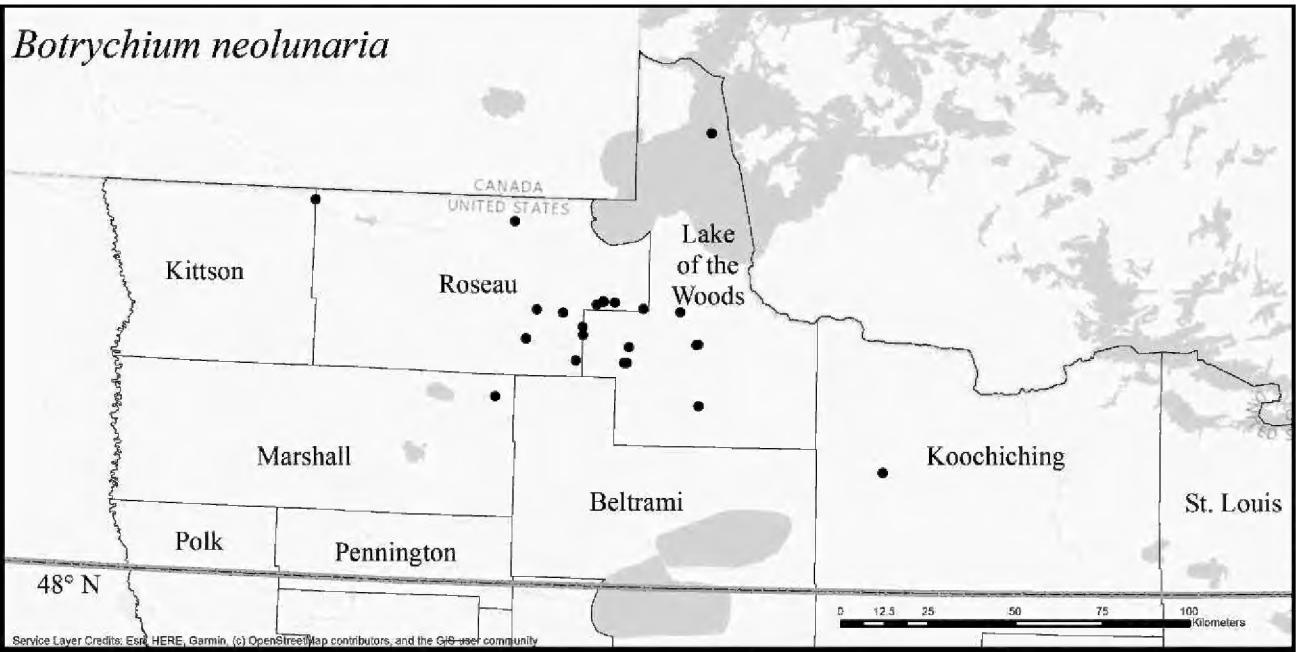


FIGURE 6. Distribution of *Botrychium neolunaria* collections in the Survey Area.

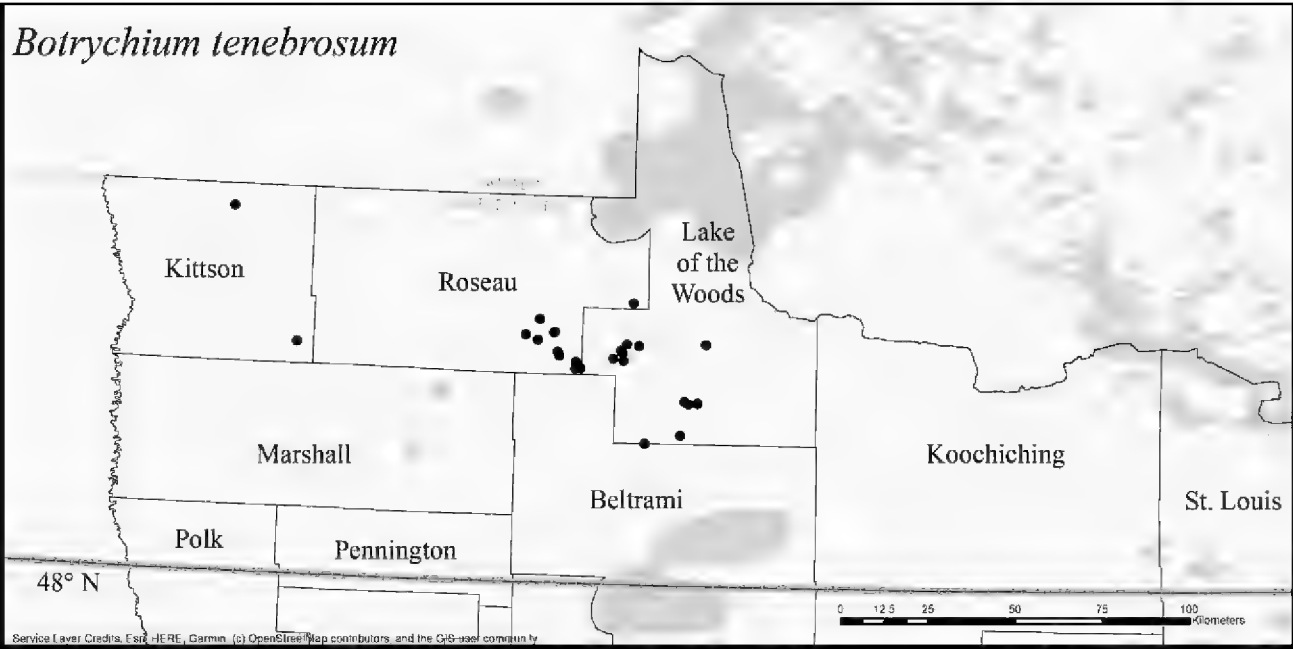


FIGURE 7. Distribution of *Botrychium tenebrosum* collections in the Survey Area.

dors, most often in an east-west orientation. This is consistent for all but the rarest *Botrychium* species in the western counties. These corridors occur along the beach ridges deposited by the receding Lake Agassiz. Between these ridges are peatland basins, not generally suitable habitats for these species.

We did not search peatlands except for transitional habitats on the margins of these and other wetlands in the hope of finding *Botrychium crenulatum*. *Botrychium tenebrosum*, another potential occurrence in select parts of these habitats, was collected from a few of these seasonally wet habitats. During the same period and beginning some years before us, the Minnesota Biological Survey had a team in this area; the botanists and plant ecologists concentrated their

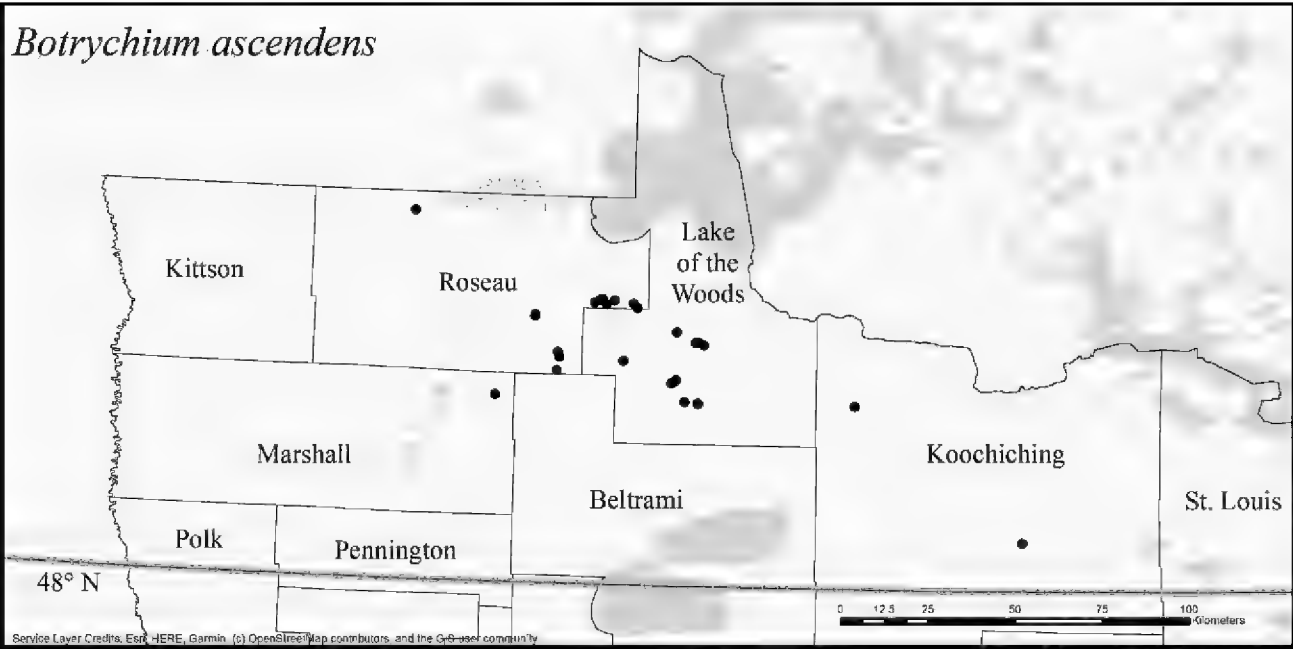


FIGURE 8. Distribution of *Botrychium ascendens* collections in the Survey Area.

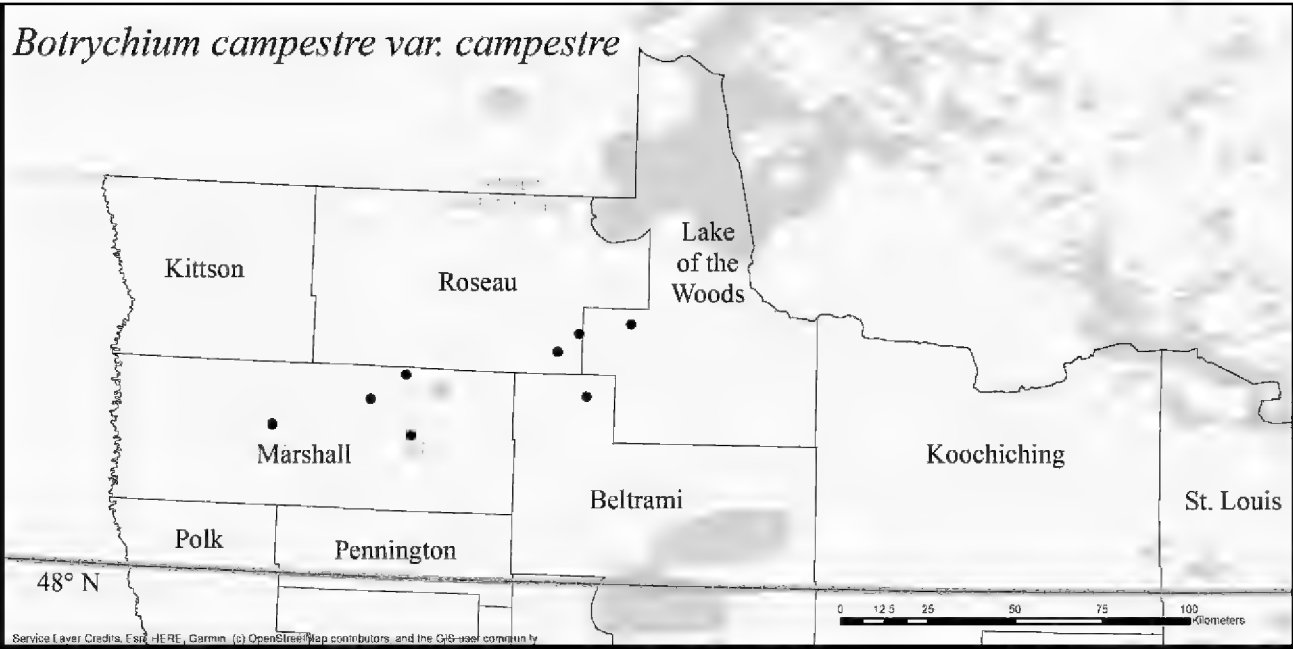


FIGURE 9. Distribution of *Botrychium campestre* var. *campestre* collections in the Survey Area.

efforts on high-quality native plant communities including these exceptional peatlands. They did not find any *Botrychium* in these communities.

DISCUSSION

The cluster of *Botrychium* occurrences in Beltrami Island State Forest and Red Lake Wildlife Management Area is likely due in large part to a unique landscape history, both pre- and post-settlement. The open-canopied *Pinus banksiana* barrens and savannas with small meadows that were the pre-settle-

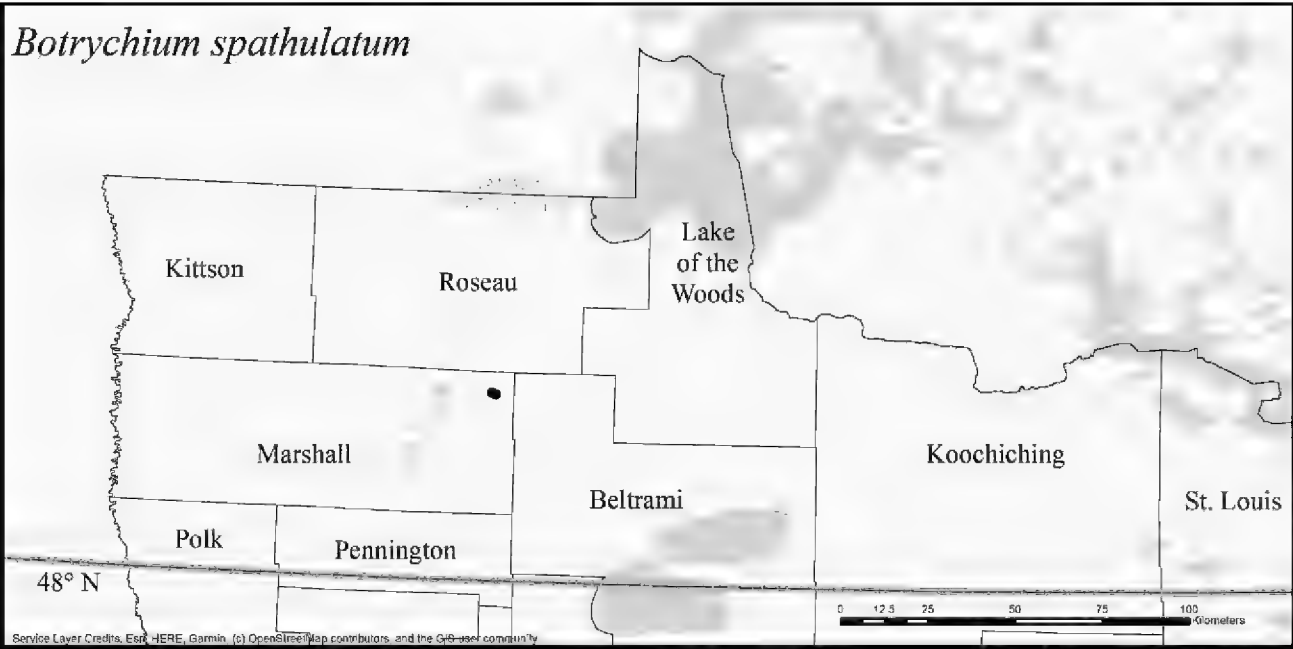


FIGURE 10. Distribution of *Botrychium spathulatum* collections in the Survey Area.

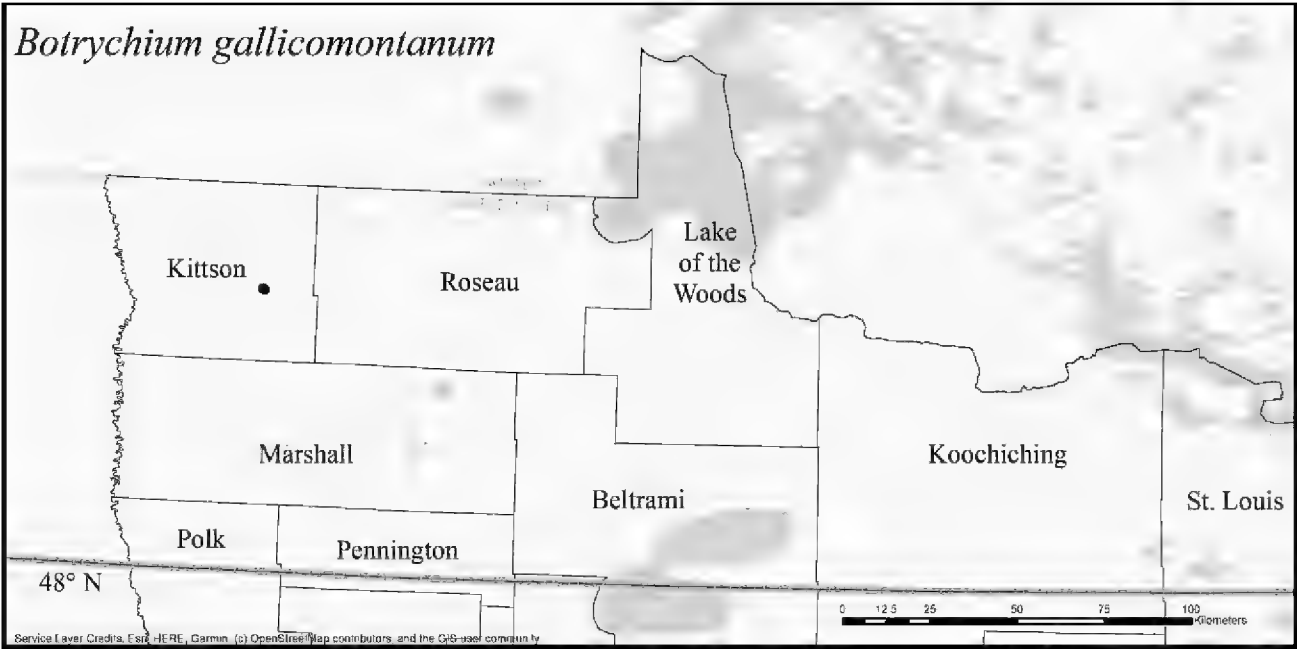


FIGURE 11. Distribution of *Botrychium gallicomontanum* collections in the Survey Area.

ment vegetation on beach ridges in central Lake of the Woods and eastern Roseau Counties were arguably the most favorable habitat for most *Botrychium* species in this region. Marschner’s (1974) map of pre-settlement vegetation shows a limited distribution of this community which is essentially identical to the distribution of clustered *Botrychium* collections today. Most effective spore dispersal is relatively local (Peck et al. 1990, Farrar 2011), so we suggest that *Botrychium* concentrations here were likely original and preserved by local dispersal to abandoned settlement openings as logging practices and fire suppression effectively eliminated the original native communities, which are now largely closed-canopy woodlands dominated by *Pinus banksiana* or *Populus tremuloides*.

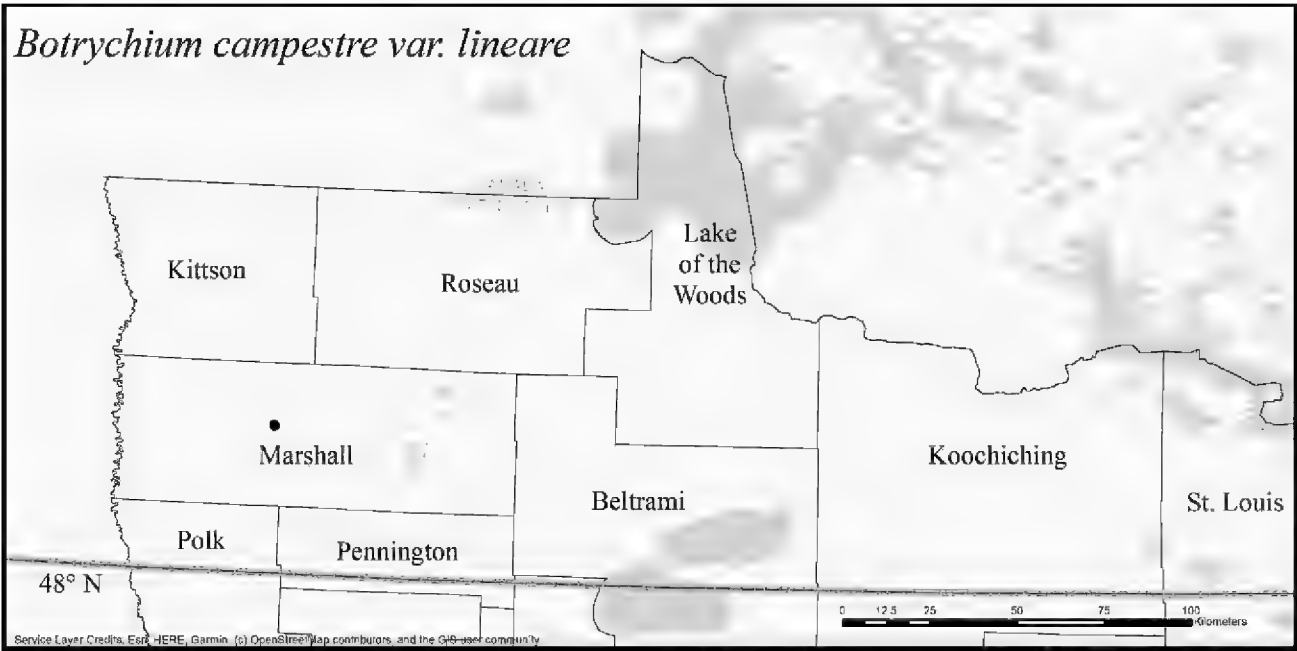


FIGURE 12. Distribution of *Botrychium campestre* var. *lineare* collections in the Survey Area.

Because the beach ridges had the most enduring settlement in the region, despite abandonment within thirty to fifty years, present distributions in large scale are likely similar to pre-settlement patterns. The actual habitats, however, are now quite different. Sustained populations through profound changes in the vegetation on this landscape would support the assertion by Farrar (2011) that a meta-population model is most prudent for *Botrychium* population dynamics and conservation.

The most productive habitats today are the old homestead sites, farmyard, and old-fields, with a mix of native and non-native species, domestic plantings and brushy encroachments on the edges. Three to six *Botrychium* species on a site are not uncommon, and some microhabitat preference is discernable in diverse sites, as are consistent associations between a few *Botrychium* species.

To the south, extending uninterrupted to the shores of the Red Lakes, are the spectacular patterned peatlands, internationally recognized for landform patterns of incomparable size and complexity (Aaseng and Djupstrom 1992). Peatlands extend to the east, sparsely crossed by beach ridges where the pre-settlement vegetation transitioned to boreal hardwood-conifer forests (Marschner 1974). Openings here were fewer, as were also settlement sites.

To the west is the prairie-forest ecotone, proceeding from wet prairie and aspen parkland to upland prairie further west. These habitats are increasingly suitable for the prairie species, but appear less so for the rest. Drainage projects were more successful to the west, so conversion to agriculture was widespread in all but the larger prairie wetlands. Remnant oak savannas tend to be the best *Botrychium* sites remaining.

Micro-distributions and Associates

While macro-distributions were essentially similar for most *Botrychium* species, micro-distributions and a few associations do suggest some differences. Roadsides, logging trails, log landings, and clear-cuts typically had sparse populations, usually *B. simplex* var. *simplex* and, less often, *B. pallidum*. Old-fields had larger populations; *B. pallidum* occurred more frequently, often with *B. matricariifolium*, *B. michiganense*, and occasionally *B. tenebrosum*. The most common associates in these open habitats include *Asters*, *Antennaria*, *Fragaria virginiana*, *Pteridium aquilinum*, *Apocynum androsaemifolium*, *Bromus*, and *Sceptridium*. None of these were particularly predictive.

The greatest diversity and abundance was most often found in the farmyards of abandoned homesteads in the immediate vicinity of foundations, plantings, and other structural remnants; these are areas marginal to the most traveled corridors in the homestead. This would suggest some influence of human traffic in augmenting the dispersal of *Botrychium* species from adjacent habitats to these settlement openings.

Within these homestead sites, there were a few associates that were consistent enough to be predictive. Old *Acer negundo* L. (Boxelder), whether in or near foundations of old structures or on the edges of old-fields, often sheltered from one to as many as five species within the span of the canopy. To the west, mixed thickets of *Prunus virginiana* L. (Choke cherry) and *Amelanchier alnifolia*

(Nutt.) Nutt. (Saskatoon) were similarly productive for one to four species. Both of these, on occasion, had species found nowhere else on the site, most often *B. minganense* and *B. neolunaria*.

When homesteads were abandoned, or settlers relocated, workers with the Civilian Conservation Corps under the Resettlement Administration would demolish structures and fill foundations, wells, and other potential hazards. In this process, slight to pronounced mounds of soil were built up around these structural remnants. A significant number of these became colonized by a near monoculture of *Bromus inermis* Leyss. with a deep mat of roots up to twelve cm thick. Often, these acquired populations of *Botrychium minganense*, *B. neolunaria*, and less often *B. pallidum*. Individuals were rooted in the mat of accumulated roots mostly or entirely above the mineral soil. The presence of *Bromus* is a virtual certainty in these homestead sites, but is not predictive for *Botrychium* in any but these most concentrated monocultures.

The most predictive associates in old homesteads were the clumps of old *Syringa vulgaris* L. (Lilac) plantings, which were very common on these sites. An estimated 60 to 70 percent of these had *B. minganense*, *B. neolunaria*, *B. pallidum*, or all three, even deep into the middle of the clump. The outer edges often sheltered other species which were likely also present in more open parts of the site.

Curiously, two of the three most predictive associates of *Botrychium* in this landscape are non-native and appear to be most often associated with the same three species. The one native species is an associate of a greater diversity of *Botrychium* species, although seemingly less predictably. Relationships between these species and the mycorrhizae could prove interesting.

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LARGE SCALE PRESENCE DETERMINANTS DO NOT NECESSARILY PREDICT INDIVIDUAL GROWTH OF AN IMPERILED DUNE THISTLE (*CIRSIIUM PITCHERI*)

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ABSTRACT

In the face of global climate change, managing imperiled species using broad sweep climate models and general distribution predictions may overlook the importance of more local determinants of success. We present a case study of the threatened dune species, *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray (Asteraceae) (Pitcher's thistle). Using both large-scale presence/absence surveys and fine-scale monitoring of growth and environmental factors using Arduino-based microclimate sensors, we determined that two of the factors that predict presence across multiple sites—high soil temperature and low soil moisture—do not necessarily correlate with the short-term growth of individuals. Our findings have implications for reintroduction schemes and local habitat management for imperiled plant species in the face of global change.

KEYWORDS: Great Lakes, Pitcher's thistle, *Cirsium pitcheri*, imperiled species, conservation

INTRODUCTION

Global climate change is exacerbating losses in biodiversity worldwide (Thomas et al. 2004; Thuiller et al. 2005). Despite efforts and some isolated successes, the number of imperiled plant species continues to rise (IUCN 2021). Understanding the determinants of the distribution of imperiled plant species will be important for predicting ecosystem changes in response to anthropogenic climate perturbation.

As plant growth zones migrate northward, plants might not migrate at the same pace (Kelly and Goulden 2008). Predicting future ranges and habitat losses will require understanding the environmental determinants of the distribution and abundance of species, but conservation biologists also need to know the relative importance of dispersal limitation and other neutral factors (e.g., chance events) that may impact local populations.

A useful starting point is to focus on imperiled species in systems that are dynamic to begin with, such as coastlines. Well-studied environmental gradients (Lichter 1998, 2000) and frequent, predictable disturbances make coastal dune systems ideal habitats for studying populations that require a mosaic of suitable habitat for long-term persistence (McEachern et al. 1994). The metapopulation

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structure of imperiled plant species inhabiting shoreline dune systems can make them particularly vulnerable to the effects of global climate change (Vitt et al. 2010; Garner et al. 2015).

We present a case study of one such species, *Cirsium pitcheri* (Torr. ex Eaton) Torr. & A. Gray (Asteraceae) (Pitcher's thistle), which is endemic to sandy shores of the three westernmost Laurentian Great Lakes. Previous studies indicate that open, dry, sandy areas are the ideal habitat for this species (Loveless 1984; McEachern et al. 1994). Therefore, we also expect those same factors to predict higher growth of individual plants in such habitats than in wetter, more vegetated areas. In our study, we first sought to confirm the environmental factors associated with *C. pitcheri* presence at several sites on a relatively unimpacted Lake Michigan island. Subsequently, we investigated the impact of these factors on the short-term growth of individuals in a naturally persisting population along a single dune system on the same island. Using both large-scale presence/absence surveys and fine-scale monitoring of individual growth and environmental factors using Arduino-based microclimate sensors, we determined that the factors that predict presence do not necessarily correlate with short-term growth.

MATERIALS AND METHODS

Study Site and Study Species

Beaver Island is the largest island in a remote archipelago situated in the northern portion of Lake Michigan (Figure 1). Similar to most linear dune systems in the Great Lakes, young Beaver Island dunes are dominated by *Ammophila breviligulata* Fern. (Poaceae) (American beachgrass) and *Calamovilfa longifolia* (Hook.) Scribn. (Poaceae) (sand reed grass) and are mostly comprised of sandy substrates (Girdler and Radtke 2006). Associated plant communities include sporadic patches of *Salix* spp. (Salicaceae) (willows), *Juniperus communis* L. (Cupressaceae) (juniper), *Prunus pumila* L. (Rosaceae) (sand cherry), and *Arctostaphylos uva-ursi* (L.) Spreng. (Ericaceae) (bearberry), with *Juncus* spp. (rushes), *Equisetum* spp. (horsetails) and *Potentilla anserina* L. (Rosaceae) (silverweed) occupying the wet swales.

Cirsium pitcheri is a federally listed threatened native plant, endemic to the dunes of the western Great Lakes, where it colonizes open sandy areas maintained by cyclic natural disturbance processes (Loveless 1984; McEachern et al. 1994). Individuals live 4 to 10 years as juvenile, non-flowering rosettes, then flower once and die (Loveless 1984). The causes for the decline of *C. pitcheri* are found at several scales. At the landscape level, sand mining, shoreline development, dune and shoreline stabilization, and disruption of shoreline currents that replenish eroded shorelines have destroyed the dune habitat of this species throughout its range (Pavlovic et al. 2002). Additionally, climate drives patterns of winter storms that can increase or decrease dune disturbance, which affects successional dynamics. Climate change may also alter lake levels over and above the change due to natural cycles (Johnston et al. 2017). Lake level changes can impact habitat availability or water availability, thereby impacting *C. pitcheri* populations. Local threats include habitat fragmentation and loss, trampling by recreational use, and invasive plant competition (Pavlovic et al. 2002). Some of these factors have been ameliorated at a few sites (Pavlovic et al. 2002); however, seed predation by a weevil (*Larinus carlinae*; previously *L. planus*) introduced for the biocontrol of weedy thistles is emerging as a new threat and is already affecting *C. pitcheri* populations (Louda et al. 2005; Havens et al. 2012). At two long term (20+ years) study sites in Wisconsin and Michigan, population growth rates are highly variable among years, but are generally below replacement ($\lambda < 1.0$; Havens et al. 2012).

Large-Scale Presence/Absence Survey

Placement of Transects

To identify the environmental variables associated with the site-level distribution of *Cirsium pitcheri*, in July and August of 2016 we conducted transect surveys in five Beaver Island dune systems

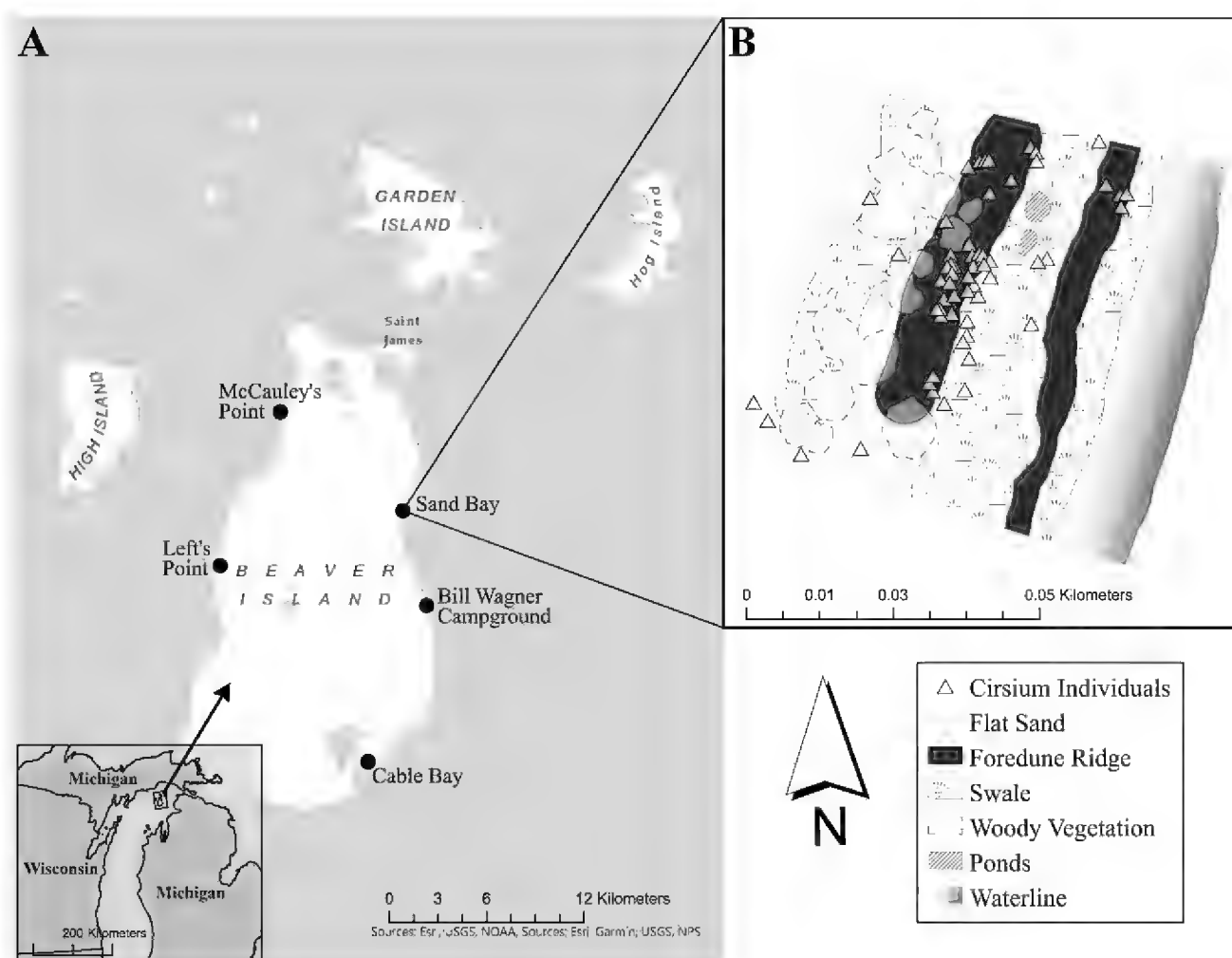


FIGURE 1. Map of survey sites located across Beaver Island. (A) Black circles represent transect survey locations. Inset (B) shows habitat features and triangles marking individually monitored plants at Sand Bay.

that were previously known to contain *C. pitcheri* (Figure 1). All of these sites can be classified as simple coastal linear dunes (Pavlovic et al. 2002), with occasional blowouts along the shore, but no perched dune systems with distinct refugia. Each site contained one pair of randomly established transects, except for Sand Bay, which contained two pairs. Transect pairs ran perpendicular to the lakeshore, starting at the shoreline and stopping at the tree line (tree height > 1 m) or a maximum length of 50 m; transects did not extend into blowout areas at any site. The location of the first transect was randomly selected from a pool of candidate locations where at least three individuals of *C. pitcheri* were present. The second transect was then placed 20 m parallel from the first in a randomly chosen direction. This sampling scheme was intentionally biased towards sites with known suitable habitat—relatively unstable sandy dunes—and did not seek to quantify range-wide distribution patterns.

Occurrence and environmental data

We recorded *Cirsium pitcheri* abundance in a 1 m² area every 2 m along each transect. Each 1 m² area was further divided into four 0.25 m² subsections, and each subsection was given a qualitative bare ground percentage cover score ranging between 0 and 6 (0 = 0%, 1 = < 5%, 2 = 5–25%, 3 = 26–50%, 4 = 50–75%, 5 = 76–95%, and 6 = > 95% bare ground cover) as seen from above. Scores for all four subsections were then averaged to produce a mean cover score for each 1 m² area of surveyed habitat. Dune slope was measured in degrees above horizontal at every sampling point using the iOS 7 Compass app on an iPhone 5c (Apple Inc, Cupertino, California).

We also measured daily soil temperature (C°) and percentage soil moisture at every 2 m interval using a Vernier Lab Quest 2 (Vernier, Beaverton, Oregon) with a Vernier soil moisture sensor and soil temperature probe. All sites had at least six consecutive days of soil measurements except Left's Point, which had only two. The main site near the field station at Sand Bay was measured every day,

and the farther sites were surveyed sequentially over four weeks. In order to account for day-to-day variation in soil moisture and soil temperature over this time period, we adjusted all values using the Sand Bay site as a reference. The daily average soil moisture values for Sand Bay were divided by the grand mean of all Sand Bay soil moisture values to create a standardizing value for each day. These standardizing values were then multiplied by the corresponding daily average soil moisture values for the other four sites to reduce the variation in soil moisture encountered when sampling multiple sites over the four-week study period. Soil temperature values for each site were adjusted using the same method.

Statistical Analysis

To determine the environmental factors associated with the distribution of *Cirsium pitcheri*, we conducted a mixed-effects multiple logistic regression in R ('lmer' package), modeling species presence as a function of fixed effects (intercept, adjusted soil moisture, adjusted soil temperature, bare ground cover, slope, and distance from the shoreline). Because our sites were chosen from among many possible sites on Beaver Island, we included site in the model as a random effect (Bolker 2015). P-values for each fixed effect were determined using the package 'lmerTest', and variance components (calculated using the delta method) were extracted using the package 'MuMIn.' Diagnostic goodness of fit plots and binned residual versus fits plots were subsequently created to assess model fit and whether model assumptions were met. A Hosmer-Lemeshow test ($p = 1.00$) and significance of deviance test ($p = 1.00$) determined that the fitted model did not significantly differ from a saturated model. A principal component analysis (PCA in the package 'ggbiplot') was then used to visualize the measured environmental niche space for *C. pitcheri*.

Fine Scale Monitoring

Study Site Monitoring

During the summer of 2017, we studied the relationship between the growth of individual *Cirsium pitcheri* plants and environmental factors at the Sand Bay site (45.68794 N, 85.505255 W). This site consists of a simple linear coastal dune system with one foredune and one secondary dune separated by a wetter swale (Figure 1 inset). We monitored growth in 60 vegetative, single-rosette plants possessing 6 to 12 leaves and continuously measured soil temperature and moisture using Arduino sensors over a six-week period. Individuals were chosen by flagging the first 100 individuals found within the study plot on Sand Bay while walking in a serpentine pattern across the first two dune ridges. We then randomly selected 60 individuals. Of these, we randomly selected 40 to be monitored by an environmental sensor (Figure 2). All leaves for each plant were measured from the rosette base to the leaf tip at the start of the study (June 22) and approximately every two weeks until the end of the study (August 1). Environmental factors that remained constant for the entirety of the study were recorded for all 60 individuals: cover, slope, aspect, distance from waterline, and position on dune. We centered a 1 m² quadrat around each selected plant and assigned it to a cover class including all vegetative and detritus material from 1 to 6, scored in the same manner as the bare ground percentage cover described above. Aspect and slope were also recorded for each plant using a compass and level phone app (Bubble Level on Huawei Honor 5x), respectively.

Sensor Design

The microclimate sensors were built using an Arduino Pro Mini 5 v 16 mHz microcontroller (Es-ooho) to continuously measure soil temperature (DS18B20 probe; Esooho), and soil moisture (YL-69 + YL-38 probe; XCSOURCE Direct) (Figure 3). A MicroSD Card Adapter (SenMod) and 8 GB MicroSD (SanDisk) card were all attached to the unit to store the data collected by the probes. Each sensor was powered by four AA batteries and contained in a plastic container with an O-ring seal (Target Corporation; Sterilite). Silicone sealant was used to fill the hole where the probes wires protruded.

On the 40 randomly selected plants, sensors were placed roughly 0.5 m north of the plant. The soil temperature and moisture probes were placed vertically into the ground to a depth of 10 cm at the base of an individual's rosette. The probes were placed parallel to the plant's taproot to avoid interference with the individual's growth.

In the sensor code, we utilized open-source resources created to operate the various probes and functions needed for the sensors to operate. Specifically, the Low Power Library by RocketScream (GitHub 2021a) was used as well as the libraries used in conjunction with each probe (soil tempera-



FIGURE 2. The setup of the sensors on the dune. A sensor was placed roughly 0.5 m north of each selected plant. The soil temperature and soil moisture probes were placed in the ground parallel with and immediately adjacent to the taproot of an individual of *Cirsium pitcheri*. In total, 40 sensors were constructed and deployed in the study plot.

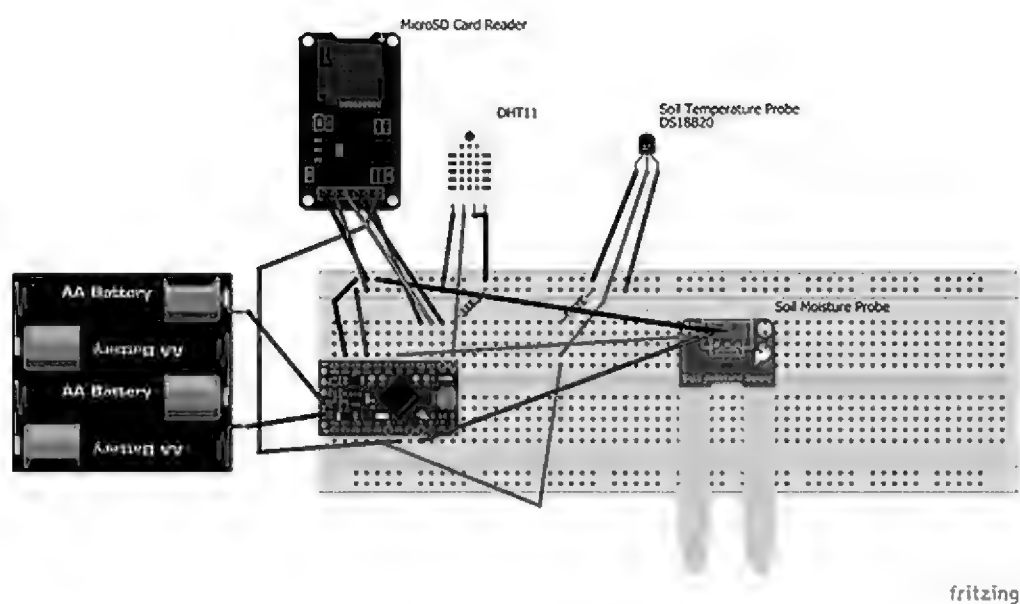


FIGURE 3. Fritzing diagram of the design of the sensors. The diagram displays each connection with each probe labeled and the Arduino Pro Mini in the center. Ambient temperature and humidity from the DHT11 probe proved inconsistent and is thus excluded from further analysis. The figure was created using Fritzing v.0.9.3 software.

ture probe: GitHub 2021b and PJRC 2021). Each sensor was coded to remain in low-power mode until it took one reading every hour. Sensor data were collected from the MicroSD cards once every two weeks as well as with periodic random spot checks of the functionality of the sensors. Start date and time were noted when individual sensors had to be repowered or replaced.

Spatial Data

The latitude and longitude were recorded for each plant using a Trimble Geo 7x Global Positioning System (GPS) mounted on a 1 m monopod. We used these data, along with mapped dune features collected with the GPS, within a geographic information system (ArcGIS v 10.3, ESRI, Redlands, California) to determine the straight-line distance of each plant to the waterline and to categorize each plant's position with respect to dune features (i.e., top of dune, swale, lake facing slope of dune, inland facing slope of dune).

Statistical Analysis

In R, we used an Augmented Dickey-Fuller ('tseries' package) test to evaluate each sensor's soil temperature data as acceptable for time series analysis. Because soil temperature oscillates over time with daily cycles, we were able to create a sine-wave model for each sensor. These models were informed by the periodicity from a periodogram. From each model we extracted the absolute value of the amplitude and the value of the y-intercept as measures of how much the soil temperature fluctuated and the general soil temperature, respectively. The sine wave model was able to cover gaps in the sensor data. We took a minimum of 50 measurements from each of the 40 sensors.

For soil moisture, we took the mean and standard deviations from the percentage of saturation over the entire six-week period for each sensor. Because soil moisture does not oscillate in daily fluctuations, we could not use a sine wave model to span gaps in sensor readings due to power loss or other factors. We therefore took a minimum of 100 measurements from each of 32 sensors.

Plant growth was measured every two weeks with three different metrics: total leaf length, average leaf length, and number of leaves. We estimated growth as the slope coefficient of a linear regression for each of these metrics over the four measurements. One individual experienced meristem damage that spurred rampant leaf growth and new leaf generation and was therefore omitted from all further analysis.

Using the 'vegan' package in R, we performed a redundancy analysis (RDA) using a matrix of environmental factors—soil temperature amplitude, soil temperature intercept, soil moisture mean, soil moisture standard deviation, cover score, percent slope, aspect, distance to waterline, and topographic position on the dune—as explanatory variables to explain our dependent variable matrix of growth estimates—total leaf length, average leaf length, and number of leaves—setting an alpha of 0.05. The model was scaled to one by eigenvalues. This analysis allowed us to include plants without sensors and those with gaps in sensor data in the same model as those with more continuous sensor data. Additionally, because of the rosette growing habit of *Cirsium pitcheri*, no one single growth metric is adequate for showing the trend of an individual due to normal leaf senescence over a growing season. Older leaves typically die as new leaves emerge. Without invasively tagging leaves, leaf turnover is difficult to measure. From the RDA model we extracted an observed F and pseudo-R².

To examine the power of our model to reveal environmental determinants of growth, we performed a randomization test with 10,000 iterations. We randomized the explanatory data matrix by shuffling the environmental factors and conducting a new RDA. The correlated measurements of soil temperature amplitude and intercept as well as the mean and standard deviations in soil moisture were kept together during the shuffling. The results from shuffled environmental matrices RDAs were used to contextualize the results from the unshuffled RDA. The simulated F-values and simulated pseudo-R² values were plotted and compared with the respective values from the actual RDA model using observed environmental data matrix. All statistical analyses were performed and graphs created with R Studio version 3.6.3.

RESULTS

Although lake levels have risen recently in the Great Lakes basin from a low in 2011, the difference in the two study years was not substantial. Lake Michi-

TABLE 1. Summary of statistics for the overall environmental conditions during the summer months, June, July, and August (JJA), at St. James on Beaver Island, Michigan. Monthly data from NOAA (2021). Precip = total precipitation for JJA; Max and Min Temp = mean of JJA maximum and minimum temperatures in Celsius; St. Dev. = standard deviation.

Year	Precip. (cm)	Max Temp. (°C)	Min Temp. (°C)
2016	24.8	23.6	14.8
2017	22.7	21.8	12.8
Mean 2008–2017	21.1	23.1	13.6
St. Dev. 2008–2017	5.14	1.15	1.12

gan-Huron elevation was 176.84 m above sea level at the July peak in 2016, and 176.99 m above sea level in July of 2017. Precipitation as measured in nearby St. James, Michigan (NOAA 2021) was lower in 2017 compared to 2016, as were maximum and minimum temperatures, but both years were within a standard deviation of the preceding 10 years (Table 1).

Large-Scale Presence/Absence Survey

Environmental data varied considerably within and between sites in our large-scale survey (Table 2). In a mixed-effects multiple logistic regression predicting *Cirsium pitcheri* presence, only soil temperature ($p < 0.05$) and moisture ($p < 0.05$) were significantly associated with the odds of finding *C. pitcheri* (Table 3). Increases in soil temperature correspondingly increased the odds of finding *C. pitcheri*, while increases in soil moisture reduced the chances of finding *C. pitcheri* in a dune environment. Bare ground cover ($p = 0.14$), slope ($p = 0.81$), and distance from the shoreline ($p = 0.67$) were not significantly associated with *C. pitcheri* presence. Fixed effects explained most of the variation in the model (27.4%); however, site as a random effect also explained a considerable amount of variation (8.7%).

In a PCA biplot visualizing the environmental niche space of *Cirsium pitcheri*, the 1 m² areas of surveyed habitat where *C. pitcheri* was present appear clustered together in the bottom right of the biplot (Figure 4). In this figure, data

TABLE 2. Summary of the statistics for the environmental data at the five large scale study sites in 2016. SD = standard deviation.

Study Site	Year	Soil Moisture (%)			Soil Temp. (°C)		
		Mean ± SD	Max	Min	Mean ± SD	Max	Min
Bill Wagner Campground	2016	6.8 ± 10.9	51.5	1.1	23.7 ± 2.2	29.3	18.1
Cable Bay	2016	3.1 ± 3.2	48.3	0.1	22.6 ± 2.5	28.7	15.3
Left’s Point	2016	4.0 ± 2.7	22.7	1.3	25.4 ± 1.7	29.0	20.4
McCauley’s Point	2016	6.7 ± 6.2	48.7	2.0	25.2 ± 2.2	30.6	19.4
Sand Bay	2016	8.4 ± 11.7	57.1	0.2	20.6 ± 2.0	25.8	15.0

TABLE 3. Summary of results for a mixed-effects multiple logistic regression predicting *Cirsium pitcheri* presence as a function of the fixed effects—intercept, adjusted soil temperature, adjusted soil moisture, bare ground cover, slope, and distance from the shoreline—along with the random effect site.

Predictor				
<i>Random effect:</i>				
Site	Variance	Std. Dev.		
	0.511	0.715		
<i>Fixed effects</i>				
	Coef. β	Std. Error (β)	z-value	p-value ($> z $)
Intercept	6.363	2.610	−2.44	< 0.05 *
Adjusted soil temperature	0.236	0.113	2.10	< 0.05 *
Adjusted soil moisture	−0.077	0.036	−2.11	< 0.05 *
Bare Ground Cover	0.169	0.114	1.48	0.14
Slope	−0.007	0.027	−0.24	0.81
Distance from the shoreline	−0.005	0.012	−0.43	0.67

points represent the distillation of many environmental variables sampled for each plot into only two: PC1 and PC2. The 95% confidence ellipse encircling plots with *C. pitcheri* present (triangles) is almost entirely within the ellipse for plots where the species is absent (circles), indicating that *C. pitcheri* is present at only a subset of plots where it could possibly be found. Species presence in re-

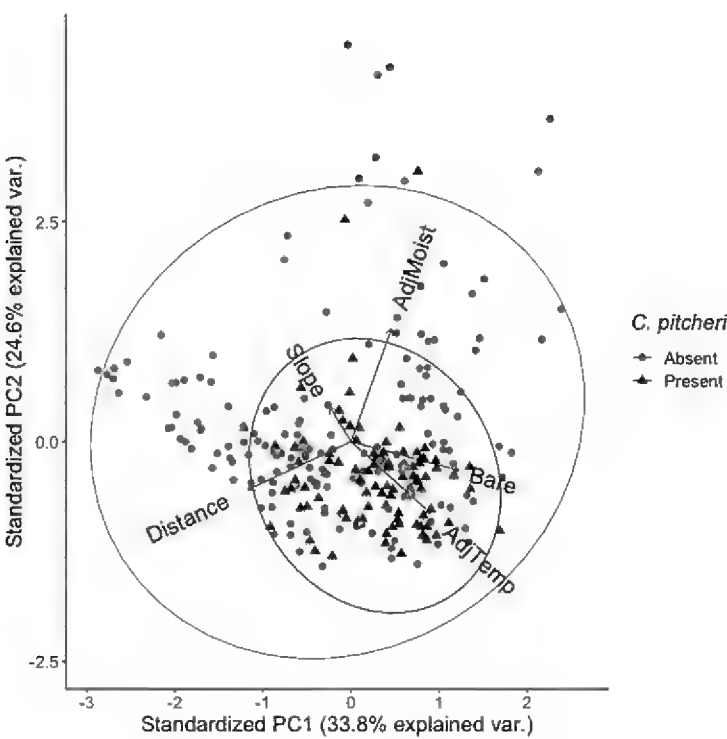


FIGURE 4. Principle component analysis (PCA) biplot indicating the loading for each measured environmental variable (AdjTemp: soil temperature adjusted as described above to account for different sampling days at different sites; AdjMoist: soil moisture values adjusted similarly; Bare: categorical variable representing bare ground present; Slope: slope in degrees of center of plot; Distance: meters from lake edge), the PCA scores for each surveyed 1m² area of dune habitat (data points represent the distillation of many environmental variables into only two: PC1 and PC2). Symbols indicate presence (dark gray, triangles) or absence (light gray, circles) of *Cirsium pitcheri* at each point along surveyed transects. Ellipses indicate the 95% confidence intervals for *C. pitcheri* presence (inner ellipse) and absence (outer ellipse).

lation to the environmental loadings (vectors in the biplot) corresponds with the results from the mixed-effects multiple logistic regression. The soil temperature vector (AdjTemp: temperature adjusted to account for different sampling days at different sites) aligns with the increased likelihood of *C. pitcheri* being present, pointing in the direction of the cluster of triangles. In contrast, the soil moisture vector (AdjMoist: moisture values adjusted similarly) aligns with decreased likelihood of *C. pitcheri* presence (away from the cluster of triangles).

Fine Scale Monitoring

At the fine scale level, both soil moisture (Mean: 14.2% saturation; SD: 8.9% saturation) and soil temperature (Mean: 21.3°C; SD: 4.8°C) varied considerably between monitored individuals. Lower temperature values compared to 2016 (Table 2) are likely due to sensors continuously monitoring through the night. Over the 6-week monitoring period, the majority of plants grew larger while some senesced (change in total leaf length: 8.9 ± 14.1 cm (Mean \pm SD); change in average leaf length: 0.3 ± 1.0 cm; change in number of leaves: 0.4 ± 1.1).

The redundancy analysis indicated that the measured environmental factors (soil temperature, soil moisture, cover score, slope, aspect, distance from waterline, and position on the dune) did not predict the growth of 60 *Cirsium pitcheri* plants ($F= 1.110$, $p=0.394$, $R^2=0.478$) (RDA triplot shown in Figure 5). By randomizing our data set 10,000 times, we simulated scenarios to show it was theoretically possible for our measured environmental variables to predict observed growth. In other words, the randomization test demonstrated that the lack of relationship between measured environmental factors and growth was not due to

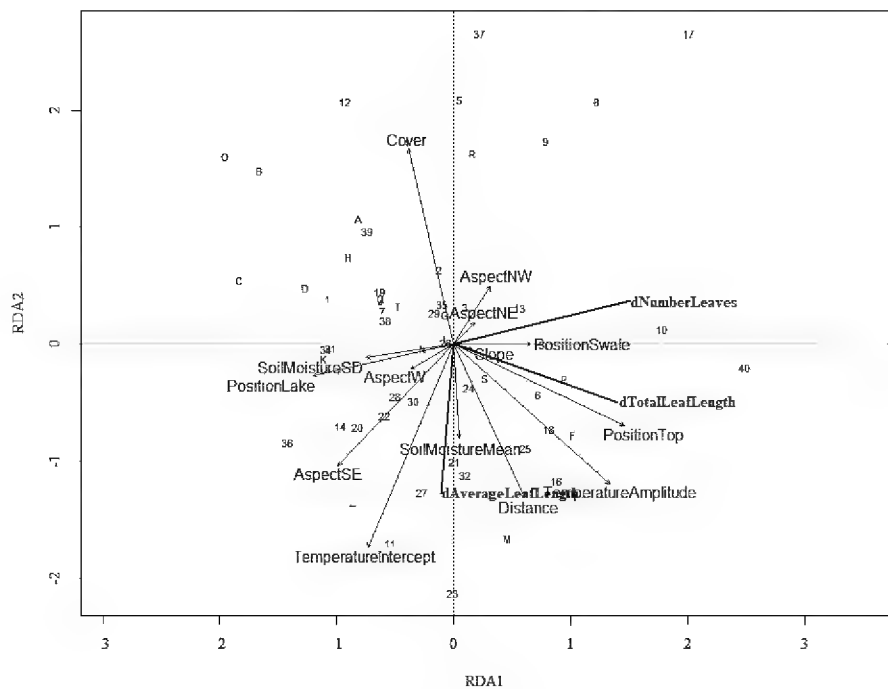


FIGURE 5. Correlation triplot of the redundancy analysis of observed data. The relationships in multidimensional space between the independent, environmental factor (thin arrows, sans-serif font) are not correlated with the dependent, growth variables (bold lines, serif font). *Cirsium pitcheri* individuals are indicated by numbers for those with a sensor ($n = 39$) and letters for those without ($n = 20$). The model was non-significant ($F= 1.110$, $p=0.394$, $R^2=0.478$).

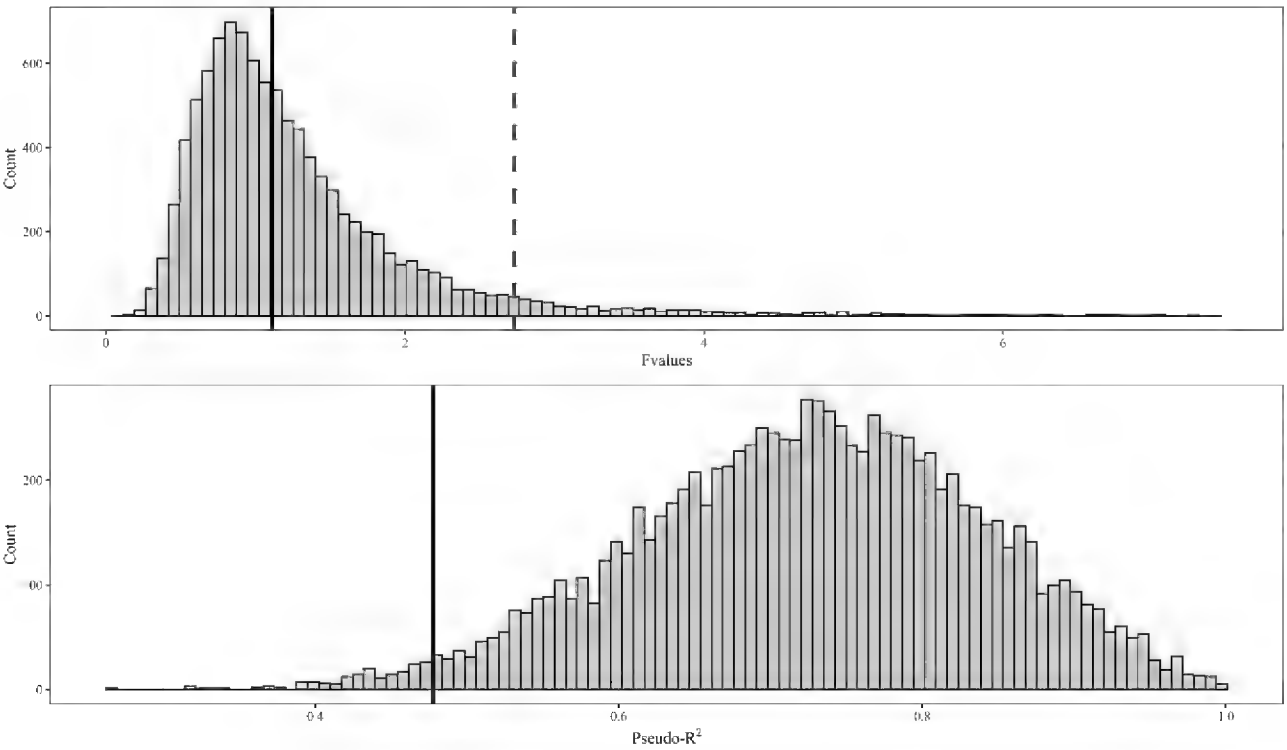


FIGURE 6. Observed RDA test statistics plotted against distributions of statistics from 10,000 randomization simulations, which show that a significant predictive relationship was theoretically possible with the current data set. **Top:** The frequency distribution of F-values. The solid black line displays the F-value from the RDA model using observed data. The dashed gray line displays the 0.05 alpha threshold (the x-axis has been truncated with 22 F-values extending past the limit of 7.5). **Bottom:** The frequency distribution of pseudo-R² values from the simulated RDAs with shuffled environmental data. The solid black line indicates the pseudo-R² from the RDA model using observed data.

the small sample size, the limited six-week observation period, excessive variation, or a limitation in the scope of our environmental data, but is more likely caused by the lack of an ecological relationship. The F-value from the original RDA using observed data fell well below the alpha (0.05); but randomized scenarios could have significantly predicted growth (Figure 6). The distribution of simulated pseudo-R² values similarly shows that more predictive relationships were feasible, with 98.1% of simulated models containing larger pseudo-R² values than the RDA on our observed values (Figure 6).

DISCUSSION

The site-scale distribution pattern shown by five populations of *Cirsium pitcheri* on Beaver Island closely matched the distribution shown by mainland populations (Loveless 1984; Halsey et al. 2015, 2017). Increasing temperature and decreasing soil moisture significantly predicted the presence of *C. pitcheri* across the island-wide survey. However, while these factors predicted *C. pitcheri* presence at a site, they did not correlate with the growth of individuals. In our fine-scale monitoring of *C. pitcheri* individuals, the suite of measured environmental factors did not predict growth within the six-week time interval. The discrepancy between our coarse and fine-grained results points out the

importance of stochastic events in the life cycle of this species. Serendipitous alignment of successful seed dispersal, followed by conditions suitable for successful germination and establishment (such as found by Rand et al. 2015), in microsite conditions that disfavor competitors (e.g., shifting sand, high soil temperatures, low surface soil moisture) may in result in the typical niche space for *Cirsium pitcheri* that we found in our coarse-grained study (Figure 4) and is congruent with other studies (Loveless 1984; McEachern et al. 1994; Pavlovic et al. 2002). However, a stochastic dispersal event in a good year for germination (e.g., a wet, warm spring) could result in a robust rosette living in a microsite where local conditions did not correlate with growth, as we found with our fine-grained study (Figure 5), especially in the short term. Admittedly, monitoring the rosettes for more weeks and over multiple years would have strengthened this study. However, our randomization tests showed the potential for significant relationships to be detected even within our six-week time frame. Additionally, the utilization of Arduino-based microclimate sensors gave us a high-resolution assessment of each individual's microclimate. We therefore suggest that the lack of association between growth and microclimate is of ecological importance rather than due to a statistical lack of power.

Previous studies have found significant associations between *Cirsium pitcheri* growth and survivorship and environmental variables such as slope, elevation, and soil moisture (Rand et al. 2015; Halsey et al. 2017). For example, Rand et al. (2015) found that surface soil moisture was important to seedling establishment but less important to post-establishment growth and probability of survival to reproduction. Instead, they suggested that access to subsurface water was more important at later life stages. Halsey et al. (2017) found that seedlings transplanted onto higher elevation sites without steep slopes had higher survival and growth. These previous studies were reintroductions—intentionally planted seeds or transplants in a single cohort—whereas our individuals dispersed and established naturally and were most likely in several different yearly cohorts. In our fine scale monitoring, our plants were also at least two years old but may have been several years older; access to deeper soil water and nutrients may allow older plants to be insensitive to surface soil conditions over short time scales.

It has been suggested that dispersal limitation is under-recognized in imperiled plant species management (Baur 2014). *Cirsium pitcheri* seeds are thought to disperse very close to the maternal plant, most within a meter (Loveless 1984); Hamzé (1998) recorded a maximum of 1.27 m. Detailed tracking of dispersal using genetic testing within a population has not been undertaken. Our results indicate that *C. pitcheri* can disperse to and establish in wet and more densely vegetated dune habitats (e.g., wet swales). Additionally, we show that established individuals are just as likely to be successful in these sites as in their more “typical” habitats. Prevalence of this species in relatively open areas with hot, dry, shifting sand may be a population level phenomenon; self-perpetuating populations with positive growth rates tend to be found in dune systems and blowouts, but within that larger habitat type, microsites may not predict success.

As we begin to tackle imperiled species management in the face of climate change, we must acknowledge that the suitable habitat for this species—and po-

tentially for others—might encompass more marginal areas than the “ideal” habitat as previously defined in the literature. Given the overall metapopulation dynamics of this Great Lakes endemic species (McEachern et al. 1994; Halsey et al. 2015), managers may want to consider less “ideal” dune habitat as potential sites for *Cirsium pitcheri* conservation and restoration, since open sandy dune sites are also attractive to human recreation activities. Shifting efforts away from harmful human activity could still help increase the survival rates even if the growing conditions are not classically defined as “ideal.” The present study gives us insight that the “best” habitat at the landscape scale might not matter for the individual. Close attention to individual fitness at the microsite scale, as in our fine scale monitoring study, may produce similar insights into other imperiled plant species subject to multiple threats, especially in the face of a changing climate.

ACKNOWLEDGMENTS

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BOTANICAL ASSESSMENT OF HIGH-QUALITY WOODLAND PARCELS IN THE UNDEVELOPED LOWELL REGIONAL GREENSPACE, KENT COUNTY, MICHIGAN

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ABSTRACT

The 2019–2023 Masterplan for the Kent County Parks includes the future development of acquired properties that have been designated as the Lowell Regional Greenspace (528 acres) occupying nearly the entirety of Section 22 of Lowell Charter Township in Kent County, Michigan. As part of an on-going botanical inventory project of the greater Grand Rapids area, we have been assessing sites that Emma Cole described over 120 years ago, along with other high-quality remnant natural areas in the region. Nine wooded sites within the Lowell Regional Greenspace property that appear to be high-quality habitat were identified for floristic inventories and floristic quality assessments during the summers of 2018 and 2019. A total of 274 species are reported for the nine wooded sites, including 241 (88.0%) native species. Three of these species are designated in Michigan as rare (one of Threatened status, two of Special Concern status). A non-metric multidimensional scaling (NMDS) was run using presence/absence floristic data from the nine woodlots to spatially compare similarities and differences among the sites. Additionally, Sørensen Index of Similarity was employed to ascertain the similarity between pairs of individual sites, which was also useful for assigning plant community types in accordance with the classification system developed by the Michigan Natural Features Inventory. Six of the wooded sites were best classified as mesic southern forest (one of which has old growth characteristics), two as dry southern forest, and one as dry-mesic southern forest. Of the nine sites, the floristic quality assessment indicated that eight of the sites are floristically important statewide, whereas one, having numerous weedy native and non-native species, was deemed to be of low to moderate value. We discovered remarkable differences in species composition among the sites, even between wooded sites we classified as the same community type. Such high-diversity in a limited space underscores the importance of preserving persisting remnant habitats, even those small in extent. This study should be useful to the Kent County Parks as they begin to develop the greenspace into parkland, and to those interested in learning more about how to assess habitat quality and diversity of remnant natural areas.

KEYWORDS: Michigan flora, biodiversity, Floristic Quality Assessment, floristic inventory, Kent County Parks, Emma Cole's *Grand Rapids Flora*

INTRODUCTION

When European immigrants and their descendants began arriving in southern Michigan from places further to the east, their appreciation of forest ecosystems contrasted notably with that of the indigenous Anishinaabeg. Europeans viewed the wooded landscape as filled with resources that could be converted into capital (money), whereas the Ottawa and Potawatomi generally taught that the forest was filled with gifts that provided for the flourishing of all creatures, humans included (Cronon 1983; Cleland 1992; Kimmerer 2013). This contrast in under-

standing is illustrated by two quotes recorded just one year apart. In 1888, the Grand Rapids Board of Trade (1888) published *Grand Rapids As It Is*, with the intention of attracting immigrants, and wrote:

It is known of all men that for many years this state has been the chief producer of pine lumber in the union; no other commonwealth has placed nearly so much nor so good pine lumber on the markets of the entire country for many years past. The gross product for 1887 was well toward five thousand million feet, valued at \$65,000,000 and this annual total will not be very largely decreased for the next decade to come . . . But yet, great as this wealth of pine has been and yet is . . . the hardwood wealth of the state, yet undeveloped, is greater than the pine wealth ever was. This hardwood wealth, consisting chiefly of beech, maple, oak, elm, ash, hickory, butternut, birch, basswood, and sycamore . . . is almost innumerable in quantity, and unsurpassed in quality. There is also a vast amount of hemlock, cedar, and other evergreen timber wealth in Western Michigan. Grand Rapids is admirably located to secure the very choicest of this forest wealth.

Just one year earlier, Andrew Blackbird (known by his people as Mackaw-de-be-nessy), a highly educated indigenous Ottawa who spent much of his childhood along the Grand River, authored *History of the Ottawa and Chippewa Indians*. In his fascinating account, Blackbird (1887) wrote:

[T]he land the Great Spirit has given us in which to live, to roam, to hunt, and build our council fires, is no more to behold . . . Our forests are gone, and our game is destroyed. Hills, groves and dales once clad in rich mantle of verdure are stripped. Where is this promised land which the Great Spirit had given to his red children as the perpetual inheritance of their posterity from generation to generation? Ah, the pale-faces who have left their fathers' land, far beyond the ocean, have now come and dispossessed us of our heritage with cruel deceit and force of arms . . . O, my father, our happiest days are o'er, and never again shall we enjoy our forest home.

These two accounts show the sharply contrasting worldviews of European colonists and Indigenous Anishinaabeg and how these different worldviews valued the wealth of Michigan's forests. The colonists understood wealth as something to be secured through the *taking* of wood products from the land. A forest that was left standing was viewed as wasted; only by clearing the land and subsequent agricultural development could wealth be secured (Michigan DNR 2008). Michigan's Native Americans, however, valued forest wealth as an *existing* ecosystem, because through its flourishing, their lives were sustained, along with the lives of many other species. To the Anishinaabeg, a forest was filled with gifts, and once harvested, those gifts and their ability to support life were sacrificed (Kimmerer 2013).

Perhaps an exception to the European perspective that a forest's value came only through destructive harvesting was the preservation of family farm woodlots. In *History of the City of Grand Rapids*, Albert Baxter (1891) wrote:

[E]ven the song birds whose music once enlivened the woods, and the wild honeybees that stored sweetness in the trees, and the wild berries, and many varieties of beautiful flowers of the forest and the openings, have dwindled away—almost gone, abashed, from the presence of the white man. And the grand natural parks and groves and thickets, of maple, and elm, and oak, and hickory, and black walnut, and linden, and pine—these have been cut away—utterly destroyed—except such occasional small patches as are needed for farm and family uses.

Woodlots were kept on most family farms because of their usefulness to the overall farming operation and because they directly provided the farm family with firewood and maple syrup (NIFA, USDA 2010). Forest patches also served as a refuge for wild game that could be hunted for meat or as a cool respite for livestock on hot summer days. Many farm families, unfortunately, also used their woodlots as long-term “storage” areas for extra fencing, old tractors, or broken machinery. Because of the high quality of soils in southern Michigan, around 80% of the forest lands were cleared for agriculture in the 1800s. The remaining 20% was mostly comprised of small and isolated forest islands, many of which were farm woodlots (Michigan Society of American Foresters 2021). In more urbanized areas where cities were expanding, the fate of forests was even worse. Trees were typically seen as obstacles to development and were clear-cut for roadways, neighborhoods, and business ventures (Belknap 1922).

These land-altering dynamics were in high gear in the late 1800s when Emma Cole was writing her flora of the Grand Rapids area (Cole 1901; Crow 2017). Cole’s highly regarded *Flora* covered 16+ townships (some 585 square miles) centered on the city of Grand Rapids, including parts of Kent and Ottawa Counties. In her book Cole (1901) laments that:

Since the district has become more thickly settled, it is undergoing rapid transformation. Much of the swampland is being drained, cleared, and utilized; forests are being deprived of their valuable timber, and uplands converted into farms. The woodlands at present consist mostly of the ‘wood-lot’ reserved by the farmer.

From Cole’s writings came the inspiration for the Emma Cole Project, which is an effort supervised by the two lead authors of this paper and based at Calvin University’s herbarium. Together with undergraduate summer research assistants, we have been inventorying and assessing sites that Emma Cole (1901) described over 120 years ago along with other high-quality remnant natural areas in the Grand Rapids region. Many of the sites we have visited have been former farm woodlots. Some of these have been of marginal natural quality, while others have proven to be exceptional representations of pre-settlement forest vegetation. As part of this project, we were asked by Kent County Parks (the department of County government established in 1924 that is tasked with establishing and maintaining parks and trails in Kent County) to evaluate the natural quality of a roughly one square mile parcel near Lowell, Michigan, that is allocated greenspace to become a future Kent County park. Although slightly outside the area that Emma Cole designated for her *Flora*, this opportunity allowed us to inventory and botanically assess nine distinct mature woodland parcels within a confined geographic area, the results of which can inform parkland development.

MATERIALS AND METHODS

Site

The Kent County Parks Masterplan 2019–2023 (Kent County Parks 2021) includes development and further acquisition of properties occupying nearly the entirety of section 22 of Lowell Charter Township (see Figure 1). This currently undeveloped land, which is referred to as Lowell Regional



FIGURE 1. Map of present and future plans for Lowell Regional Greenspace. From Kent County Parks (2021).

Greenspace, is bounded on the north by 36th Street, on the south by Cascade Road, on the east by Segwun Avenue, and on the west by Alden Nash Avenue.

Initial land acquisition by Kent County Parks began in 1999 and the property currently covers an area of 528 acres. The greenspace property includes open fields, rolling wooded hills and ravines, two pristine open shrub-dominated wetlands, a Silver Maple swamp, and a large open old-field site. Some management has already begun, including a 30-acre prairie restoration project initiated in an old agricultural field (Figure 1), for which prescribed burns were conducted in 2010 and 2017. The Lowell Regional Greenspace will eventually host an equestrian facility and bridle trails, including a connecting trail to the new Kent County Youth Fair Grounds situated about 1.25 mi. eastward that now occupies the old Deer Run Golf Course on Cascade Road just north of Pratt Lake. To date, Kent County Parks has not yet begun construction of any of the facilities proposed in the master plan.

The property is contiguous to the Bradford Dickinson White Nature Preserve which is located on the north side of 36th Street and is owned and actively managed by the Land Conservancy of West Michigan. The B. D. White Preserve has similar woodland ecosystems and an extensive southern shrub-carr wetland habitat that is fed by a stream emerging from the two high quality shrub-dominated wetland areas in the Lowell Regional Greenspace site (Stockdale et al. 2019). Together Lowell Regional Greenspace and B. D. White Preserve parcels offer a significant area of preserved woodland and wetland habitat that will only increase in value from a conservation standpoint as development progresses in the vicinity.

Botanical Inventory

Botanical inventories were conducted mid-March through September 2018 and 2019 within the Lowell Regional Greenspace for nine distinct wooded research sites, selected because they appeared to retain significant elements of pre-settlement habitat (Figure 2). Two rather pristine shrub-dominated wetlands (Figure 2, EW and WW) and a Silver Maple swamp (SMS) also occur within the greenspace; inventories of these sites will be reported in a subsequent paper.

Our sampling protocol in each of these inventoried sites was a meander-search through the entire

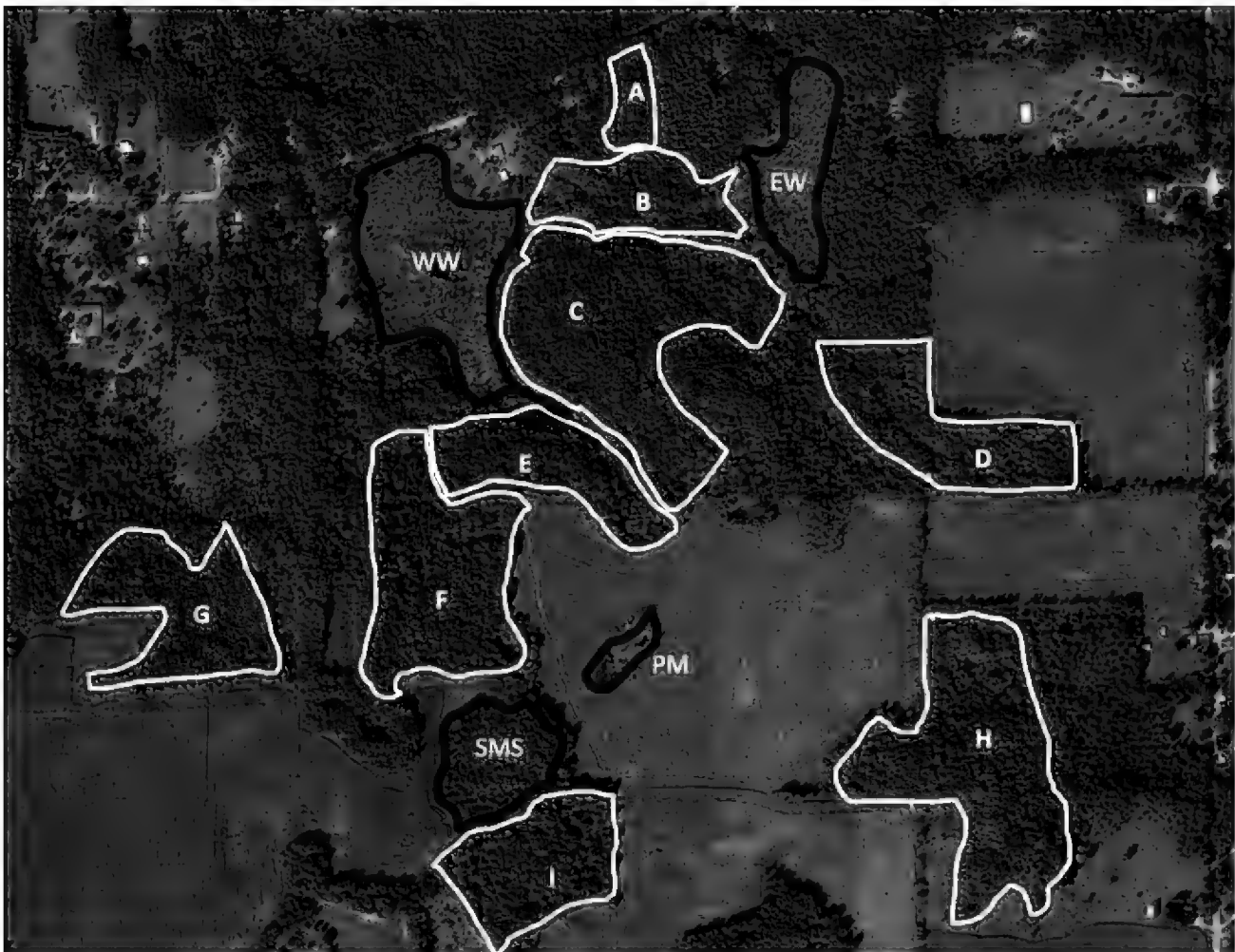


FIGURE 2. Locations of the nine Lowell Regional Greenspace woodland study sites, outlined in white. These are: A = Gateway Woods; B = North Woods; C = Dry Woods; D = Ravine Woods; E = Old Growth Woods; F = Middle Woods; G. West Woods; H = East Woods; I = South Woods. Wetlands mentioned in the text are outlined in black. These are: EW = East Wetland; WW = West Wetland; SMS = Silver Maple Swamp; PM = Prairie Marsh and Pond. (Image: 9/25/2014; source: Google).

site multiple times over the course of the growing season, keeping a sharp eye out for any microhabitats within. Particular attention was paid to areas within these sites that appeared to support high diversity. During site visits all plant species encountered were recorded as sight records and/or documented by specimens. A total of 449 herbarium specimens were collected to document the flora, especially if they had flowering or fruiting material. The first set of voucher specimens documenting the study were deposited in the Calvin University Herbarium (CALVIN), with duplicate specimens deposited in the herbaria of Michigan State University (MSC) and/or University of Michigan (MICH). Identifications were made primarily using Voss and Reznicek (2012) for seed plants and Palmer (2018) for pteridophytes. We also accessed various online resources such as MICHIGAN FLORA ONLINE (2011) and Go Botany (Native Plant Trust 2019). Nomenclature follows that of MICHIGAN FLORA ONLINE (2011), as this source includes both seed plants and pteridophytes and is frequently updated with taxonomic and nomenclatural changes.

Floristic Quality Assessments

Floristic Quality Assessment (FQA) values were obtained for each woodland site following the methodology described by Freyman et al. (2016) and Reznicek et al. (2014) using the online Universal FQA Calculator (Freyman 2016). Floristic Quality Assessments provide an extremely practical and useful metric-based measure to evaluate habitat conservation values, and have become increasingly influential in North America within the last 20 years (Spyreas 2019). The Floristic Quality Assessment tool assigns each native Michigan species a Coefficient of Conservatism (C) ranging from

0 to 10 (Reznicek et al. 2014). The C-value reflects a given species’ fidelity to undisturbed habitats. Plants with C-values of 8–10 indicate a very strong affinity to a narrow range of undisturbed ecological conditions, whereas C-values of 0–2 are associated with more widespread, disturbance-tolerant species that can be found growing in a wide range of habitats. After calculating the Mean C (\bar{C}) for each site inventoried, which is the average of the C-values of the species in that site, a Native Floristic Quality Index (FQI) for the entire site is calculated as follows:

$$FQI = \bar{C} \times \sqrt{n}$$

where n is the number of native species at the site. Hence, the Floristic Quality Index provides a reliable indication of the natural quality of an area and can be used to compare the ecological integrity of different landscapes (Bried et al. 2013). The Universal FQA Calculator generates a Native FQI and a Total FQI, the former based only on the native species present at the locality inventoried (as described above) and the latter on both native and non-native species. Inclusion of non-native species (C-value = 0) (to obtain a Total Mean C) for the calculation of a Total FQI results in a lowered overall FQI, which gives a comparative indication of the impact of non-native species on the site’s floristic quality.

The online Universal FQA Calculator also generates an Adjusted FQI score, which was first introduced in a study conducted within forested wetlands of central Pennsylvania (Miller and Wardrop 2006). One fundamental problem with the Total FQI calculation is the strong influence of species richness (which often reflects within-site habitat diversity). The Adjusted FQI corrects the index downwards for habitats with high native species richness but a low Mean C value. The Adjusted FQI also shifts the index upwards for habitats that have a lower native species richness but a high Mean C value. The Adjusted FQI formula is as follows:

$$\left(\frac{\bar{C}}{10} \times \frac{\sqrt{N}}{\sqrt{N+A}} \right)$$

where C is the Mean C value, N is the number of native species, and A is the number of non-native species.

Non-metric Multidimensional Ordination (NMDS)

A non-metric multidimensional scaling (NMDS) was run on presence/absence floristic data from the nine woodlots as a spatial way to compare similarities and differences among the sites (Figure 3). Jaccard’s dissimilarity metric is especially helpful in comparing binary data. To run the NMDS, R (R Core Team 2020) version 4.4.1 was used with the package’s *vegan* (Oksanen et al., 2020) and *MASS* (Venable and Ripley, 2002) options. The ordination was created using the *ggplot2* (Wickham, 2016) and *cowplot* (Wilke, 2020) packages. A *post hoc* test was not run because the data are binary (either present or absent) and there were no groupings except by sites.

Similarity Index

In addition to the Jaccard’s dissimilarity ordination described above, we used the Sørensen Index of Similarity (Mueller-Dombois and Ellenberg 1974) to quantitatively compare the floristic lists among each of the woodland sites studied. This approach allowed us to evaluate whether these floristic lists effectively describe the same woodland habitat type. The Sørensen Index is calculated as follows:

$$\text{Sørensen Index} = [2C \div (A+B)] \times 100\%,$$

where C is the number of shared species between the two sites, and A and B are the numbers of species in each of the two sites, respectively. An Index value of 50% or more indicates that the two sites are likely the same plant community type (Curtis 1959; Bradley and Crow 2010).

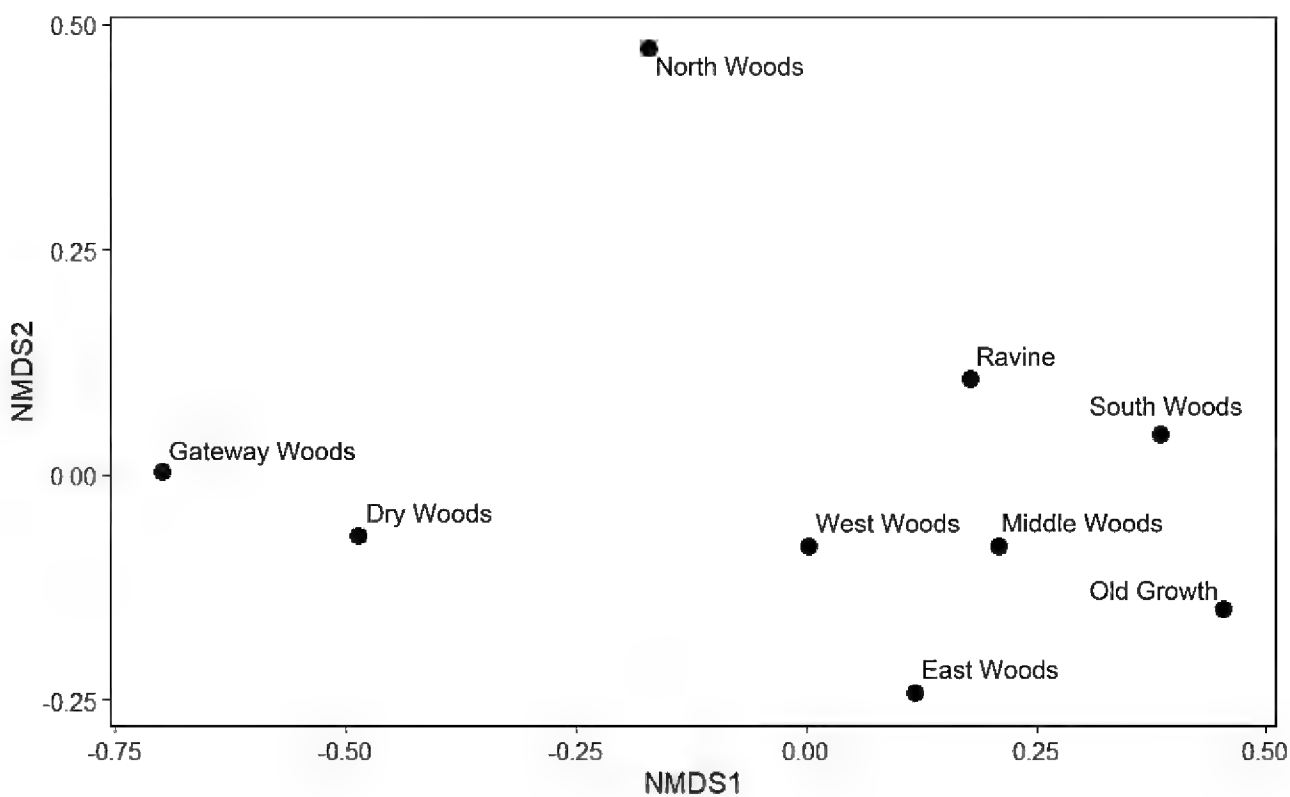


FIGURE 3. NMDS ordination demonstrating the relative similarity of the nine sites using a Jaccard distance metric. Points are labeled with the name of each site. Stress = 0.0455.

RESULTS AND DISCUSSION

Floristic Quality Assessments (FQA) Overview

As a consequence of logging, agricultural development, and urban growth, large sectors of the Michigan landscape have been significantly altered from their pre-settlement condition. Much of our native biota has become severely restricted to small, isolated tracts of natural landscapes, which have themselves been impacted by growth and development, and, according to Herman et al. (2001), principal elements of our natural ecosystems are poorly represented in the state’s present landscape. Thus, any site with a Native FQI score of 35 or higher is valued as floristically important statewide. FQI scores greater than 50 indicate exceptional sites with extremely high conservation value. Matthews et al. (2005) and Slaughter et al. (2015), while recognizing that the FQI values are useful, feel that the Mean *C* values represent a less biased indicator of relative site conservation value. We consider both metrics to be helpful for practitioners involved in ecological integrity assessments.

Individual Site Assessments

Among the nine wooded sites inventoried in 2018 and 2019 (identified as A through I in Figure 2), the Total Floristic Quality Index (Total FQI) values (see Table 1) ranged from a low of 26.9 (Total Mean *C* = 2.7) at Gateway Woods, which is the site with the highest percentage of non-native species (18.2%), to a

TABLE 1. Floristic Quality Assessment metrics for the nine woodland sites.

Site Name (Forest Community)	Area	Total FQI	Native FQI	Adjusted FQI	Total Mean C	Number of Species	Number of Native Species (percentage)	Number of Non-native Species (percentage)
Gateway Woods (Dry Southern Forest)	0.49 ha 1.20 acres	26.9	29.7	29.8	2.7	99	81 (81.8%)	18 (18.2%)
North Woods (Dry-Mesic Southern Forest)	2.56 ha 6.33 acres	43.8	45.4	40.5	3.9	126	117 (92.9%)	9 (7.1%)
Dry Woods (Dry Southern Forest)	5.64 ha 13.95 acres	34.1	36.5	39.5	3.7	85	75 (88.2%)	10 (11.8%)
Ravine Woods (Mesic Southern Forest)	7.46 ha 18.43 acres	39.3	41.0	42.8	4.1	92	87 (94.6%)	5 (5.4%)
Old Growth Woods (Mesic Southern Forest)	2.56 ha 6.25 acres	33.2	34.3	47.6	4.6	52	49 (94.2%)	3 (5.8%)
Middle Woods (Mesic Southern Forest)	5.27 ha 13.01 acres	29.2	31.0	38.1	3.6	66	60 (90.9%)	6 (9.1%)
West Woods (Mesic Southern Forest)	6.20 ha 15.31 acres	30.8	32.2	37.7	3.6	73	65 (89.0%)	8 (11.0%)
East Woods (Mesic Southern Forest)	7.65 ha 18.92 acres	34.2	35.5	37.5	3.6	90	83 (92.2%)	7 (7.8%)
South Woods (Mesic Southern Forest)	2.57 ha 6.36 acres	30.5	31.3	41.1	4.0	58	53 (91.4%)	5 (8.6%)

high of 43.8 (Total Mean $C = 3.9$) at North Woods, where the percentage of non-native species is only 7.1%. Descriptions of these nine wooded sites, all within close proximity to each other, bring to light many resemblances. However, we found it noteworthy that each parcel held its own distinctness as well, an observation we address more fully below in the Conclusion. The Floristic Quality Assessment metrics for each of these nine sites are given in Table 1, and the species recorded from each site are listed in Table 2. The forest community classification follows that of the Michigan Natural Features Inventory (Cohen et al. 2015).

Gateway Woods (42° 54.065'N, 85° 21.363'W)

Gateway Woods (A in Figure 2) is a narrow parcel that gives access from 36th Street to the Lowell Regional Greenspace property. This open woodland parcel seems to best fit a dry southern forest community type. A total of 99 species, of which 81.8% (81 species) are native, were cataloged here. Among all the woodland sites inventoried, this site had the lowest Total FQI value (26.9) and likewise the lowest Total Mean C value (2.7); since these values are indicative of disturbance, it is a site of relatively low conservation value.

Gateway Woods can be subdivided into two areas: the northernmost wooded area adjacent to 36th Street and the more southerly, somewhat open, hillside sloping down toward a creek and its floodplain. The wooded area is dominated by *Quercus velutina*, *Pinus strobus*, and *Sassafras albidum* with an understory characterized by *Cornus alternifolia*, *Chimaphila maculata*, *Diphysastrum digitatum*, *Carex pensylvanica*, *Dichanthelium depauperatum*, *D. commonsianum*, *D. oligosanthes*, and *Osmorhiza longistylis*.

The southern somewhat open, dry sandy hillside has little canopy cover with only *Quercus velutina* saplings, a small stand of *Populus grandidentata*, scattered *Juniperus virginiana*, and the shrubs *Rubus occidentalis*, *R. allegheniensis*, *R. flagellaris*, *R. pensilvanicus*, and *Corylus americana*. There are several other species typical of open dry sites that are present in the area, including *Monarda punctata*, *Euphorbia corollata*, *Apocynum cannabinum*, *Rudbeckia hirta*, *Vicia villosa*, *Fragaria virginiana*, *Oenothera biennis*, *Dichanthelium* spp., and *Solidago canadensis*.

Overall, there is a high diversity of both native and non-native plants in the small-sized Gateway Woods. The relatively high proportion of non-native weedy species (18 species or 18.2%) attests to a moderate degree of disturbance: *Achillea millefolium*, *Berteroa incana*, *Bromus inermis*, *Verbascum thapsus*, and the rather despised *Alliaria petiolata*, as well as a recently spreading invasive vine, *Vincetoxicum nigrum*. The location of this woods immediately alongside 36th Street likely accounts for the high number of weedy natives and non-native species. There also seems to be routine human disturbance as is evident by a deer hunting blind that overlooks the open slope. The southern portion of the parcel grades down to an abrupt change in vegetation (North Woods) and is bounded on the east side by a two-track separating it from a strip of planted Red Pine (*Pinus resinosa*) on private land.

North Woods (42° 54.000'N, 85° 21.341'W)

We classified the North Woods (B in Figure 2) as dry-mesic southern forest.

TABLE 2. Floristic composition of each of the nine woodland study sites at Lowell Regional Greenspace. An X indicates the presence of a species at a given site. The right-hand column gives the number of sites from which each species was recorded. State-listed species are indicated in boldface as follows: T = Threatened; SC = Special Concern.

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Acer negundo</i> L. Box Elder	X	X		X						3
<i>Acer nigrum</i> F. Michx. Black Maple			X	X		X	X	X		5
<i>Acer rubrum</i> L. Red Maple		X		X	X	X	X	X	X	8
<i>Acer saccharinum</i> L. Silver Maple				X		X				2
<i>Acer saccharum</i> Marshall Sugar Maple		X	X	X	X	X	X	X		6
<i>Achillea millefolium</i> L. Yarrow	X									1
<i>Actaea pachypoda</i> Elliott White Baneberry, Doll's Eyes		X	X			X	X	X	X	6
<i>Adiantum pedatum</i> L. Maidenhair Fern							X			1
<i>Agrimonia gryposepala</i> Wallr. Tall Agrimony	X	X	X	X	X				X	6
<i>Agrostis gigantea</i> Roth Redtop		X								1
<i>Agrostis perennans</i> (Walter) Tuck. Autumn Bent, Upland Bent									X	1
<i>Alliaria petiolata</i> (M. Bieb.) Cavara & Grande Garlic Mustard	X			X	X	X	X	X	X	7
<i>Allium burdickii</i> (Hanes) A. G. Jones Wild Leek							X			1
<i>Allium tricoccum</i> Aiton Ramps, Wild Leek						X	X			2

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TABLE 2. (Continued)

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Amelanchier laevis</i> Wiegand			X							1
Smooth Shadbush										
<i>Amphicarpaea bracteata</i> (L.) Fernald										
Hog-peanut		X			X			X		3
<i>Anemone virginiana</i> L.										
Thimbleweed		X								1
<i>Apios americana</i> Medik.										
Groundnut, Indian-potato		X								2
<i>Apocynum androsaemifolium</i> L.										
Spreading Dogbane									X	1
<i>Apocynum cannabinum</i> L.										
Indian-hemp	X									1
<i>Arcium minus</i> Bernh.										
Common Burdock					X	X		X		3
<i>Arisaema triphyllum</i> (L.) Schott										
Jack-in-the-pulpit, Indian-turnip		X	X	X		X	X	X		6
<i>Asarum canadense</i> L.										
Wild-ginger		X						X		2
<i>Asclepias incarnata</i> L.										
Swamp Milkweed				X						1
<i>Asclepias syriaca</i> L.										
Common Milkweed										
<i>Asplenium platyneuron</i> (L.) D. C. Eaton	X									1
Ebony Spleenwort										
<i>Athyrium filix-femina</i> (L.) Roth	X				X				X	3
Lady Fern										
<i>Barbarea vulgaris</i> R. Br.		X								1
Yellow Rocket				X						
<i>Berberis thunbergii</i> DC.										
Japanese Barberry		X	X					X		3

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TABLE 2. (Continued)

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Carex davisi</i> Schwein. & Torr. (SC) Davis' Sedge				X						1
<i>Carex gracillima</i> Schwein. Sedge		X	X			X	X	X	X	6
<i>Carex granularis</i> Willd. Sedge									X	1
<i>Carex grayi</i> J. Carey Sedge				X		X		X		3
<i>Carex grisea</i> Wahlenb. Sedge				X				X		2
<i>Carex hirtifolia</i> Mack. Sedge				X						1
<i>Carex hitchcockiana</i> Dewey Sedge				X				X		2
<i>Carex intumescens</i> Rudge Sedge		X								1
<i>Carex jamesii</i> Schwein. James' Sedge			X	X			X			3
<i>Carex laxiflora</i> Lam. Sedge			X				X	X		3
<i>Carex lupulina</i> Willd. Sedge				X						1
<i>Carex pedunculata</i> Willd. Sedge								X		1
<i>Carex pennsylvanica</i> Lam. Pennsylvania Sedge					X			X	X	6
<i>Carex prasina</i> Wahlenb. Sedge								X		1
<i>Carex radiata</i> (Wahlenb.) Small Straight-styled Wood Sedge						X				1

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TABLE 2. (Continued)

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Elymus virginicus</i> L.				X						1
Virginia Wild-rye										
<i>Epifagus virginiana</i> (L.) Bart.							X			1
Beech-drops										
<i>Epipactis helleborine</i> (L.) Crantz			X			X	X			3
Helleborine										
<i>Equisetum arvense</i> L.						X		X		4
Common Horsetail	X	X								
<i>Erigeron annuus</i> (L.) Pers.										
Daisy Fleabane	X	X		X						3
<i>Euonymus obovatus</i> Nutt.										
Running Strawberry-bush		X					X	X		1
<i>Eupatorium perfoliatum</i> L.										
Boneset		X								1
<i>Euphorbia corollata</i> L.										
Flowering Spurge	X									1
<i>Eurybia macrophylla</i> (L.) Cass.										
Large-leaved Aster, Big-leaved Aster	X	X		X	X			X	X	6
<i>Eutrochium maculatum</i> (L.) E. E. Lamont										
Joe-Pye-weed	X	X								2
<i>Fagus grandifolia</i> Ehrh.										
American Beech		X	X	X	X	X	X	X	X	8
<i>Festuca subverticillata</i> (Pers.) E. B. Alexeev										
Nodding Fescue		X			X			X	X	4
<i>Floerkea proserpinacoides</i> Willd.										
False Mermaid			X							1
<i>Fragaria virginiana</i> Mill.										
Wild Strawberry	X									1
<i>Fraxinus americana</i> L.										
White Ash				X						1

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TABLE 2. (Continued)

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Osmorhiza claytonii</i> (Michx.) C. B. Clarke										
Hairy Sweet-cicely	X	X								2
<i>Osmorhiza longistylis</i> (Torr.) DC.										
Smooth Sweet-cicely	X				X				X	3
<i>Osmunda regalis</i> L.										
Royal Fern		X								1
<i>Osmundastrum cinnamomeum</i> (L.) C. Presl										
Cinnamon Fern		X								1
<i>Ostrya virginiana</i> (Mill.) K. Koch										
Ironwood, Hop-hornbeam			X			X		X		4
<i>Oxalis stricta</i> L.										
Yellow Wood-sorrel	X									1
<i>Packera aurea</i> (L.) Á. Löve & D. Löve										
Golden Ragwort		X								1
<i>Packera glabella</i> (Poir.) C. Jeffrey										
Butterweed, Yellowtop					X					1
<i>Parthenocissus quinquefolia</i> (L.) Planch.										
Virginia Creeper	X	X	X	X	X	X	X	X	X	9
<i>Penstemon hirsutus</i> (L.) Willd.										
Hairy Beard-tongue	X									1
<i>Persicaria amphibibia</i> (L.) Delabare										
Water Smartweed				X						1
<i>Persicaria virginiana</i> (L.) Gaertn.										
Jumpseed	X	X	X	X	X	X	X	X	X	9
<i>Phalaris arundinacea</i> L.										
Reed Canary Grass		X								1
<i>Phlox divaricata</i> L.										
Wild Blue Phlox			X					X		2
<i>Phryma leptostachya</i> L.										
Lopseed	X	X							X	3

TABLE 2. (Continued)

Species	Gateway Woods							Species of sites			
	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods			
<i>Prenanthes altissima</i> L. Tall White Lettuce	X	X		X	X		X		5		
<i>Prunella vulgaris</i> L. Self-heal, Heal-all	X								1		
<i>Prunus cerasus</i> L. Pie Cherry, Sour Cherry		X							1		
<i>Prunus serotina</i> Ehrh. Wild Black Cherry	X	X	X		X	X	X	X	8		
<i>Prunus virginiana</i> L. Choke Cherry				X	X			X	3		
<i>Pteridium aquilinum</i> (L.) Kuhn Bracken Fern	X							X	2		
<i>Pyrola elliptica</i> Nutt. Large-leaved Shinleaf	X								1		
<i>Quercus alba</i> L. White Oak	X		X	X			X	X	6		
<i>Quercus bicolor</i> Willd. Swamp White Oak							X		1		
<i>Quercus macrocarpa</i> Michx. Bur Oak	X								1		
<i>Quercus rubra</i> L. Red Oak	X		X	X	X	X	X	X	7		
<i>Quercus velutina</i> Lam. Black Oak	X		X					X	3		
<i>Ranunculus abortivus</i> L. Small-flowered Buttercup											
<i>Ranunculus hispidus</i> Michx. Swamp Buttercup			X				X	X	3		
<i>Ranunculus recurvatus</i> Poir. Hooked Crowfoot	X								1		
							X		1		

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TABLE 2. (Continued)

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Sassafras albidum</i> (Nutt.) Nees										
Sassafras	X	X	X		X	X		X	X	7
<i>Scirpus atrovirens</i> Willd.										
Bulrush		X								1
<i>Scutellaria lateriflora</i> L.										
Mad-dog Skullcap		X								1
<i>Smilax ecirrata</i> (Kunth) S. Watson										
Upright Carrion-flower								X		1
<i>Smilax illinoensis</i> Mangaly										
Carrion-flower	X	X								2
<i>Solidago caesia</i> L.										
Bluestem Goldenrod		X	X	X	X	X		X	X	7
<i>Solidago canadensis</i> L.										
Canada Goldenrod	X	X		X	X		X			5
<i>Solidago flexicaulis</i> L.										
ZigZag Goldenrod								X		1
<i>Solidago uliginosa</i> Nutt.										
Bog Goldenrod		X								1
<i>Sphenopholis intermedia</i> (Rydb.) Rydb.										
Slender Wedgegrass								X		2
<i>Spiraea alba</i> Du Roi					X					1
Meadowsweet		X								
<i>Staphylea trifolia</i> L.										
Bladdernut			X	X						2
<i>Stellaria longifolia</i> Willd.										
Long-leaved Chickweed									X	2
<i>Symphotrichum lateriflorum</i> (L.) Á. Löve & D. Löve	X									
Calico Aster				X						1
<i>Symplocarpus foetidus</i> (L.) Nutt.										
Skunk-cabbage		X				X		X		3

TABLE 2. (Continued).

Species	Gateway Woods	North Woods	South Woods	East Woods	West Woods	Middle Woods	Growth Woods	Ravine Woods	Dry Woods	Species of sites
<i>Vicia villosa</i> Roth										
Hairy Vetch	X									1
<i>Viola canadensis</i> L.										
Canada Violet		X	X		X	.	X			5
<i>Viola rostrata</i> Pursh										
Long-spurred Violet								X		1
<i>Vitis riparia</i> Michx.										
River-bank Grape	X	X		X	X	X	X	X	X	8
<i>Zanthoxylum americanum</i> Mill.										
Prickly-ash	X		X	X	X	X		X		6
TOTALS	99	126	58	90	73	66	52	92	85	-

A total of 126 species, of which 92.9% (117 species) are native, were found in this relatively small parcel. It is the most diverse and species-rich of all the woodland sites inventoried. The Total FQI of North Woods is 43.8, and the Native FQI is 45.4, giving it the highest FQA of our forested parcels and ranking the woods as having high conservation quality (Table 1); its Mean *C* value is 3.9. North Woods consists of undisturbed forest on relatively flat terrain at the base of the disturbed southern slope of Gateway Woods (A in Figure 2) and the adjacent privately owned red pine plantation. It is bordered on the south by the north-facing slope of a very dry hillside in Dry Woods (C in Figure 2). A stream flows westward through this section of forest from one area of southern shrub-carr wetland (East Wetland; EW in Figure 2) into West Wetland (WW).

The woody species that characterize this site are *Acer rubrum*, *A. negundo*, *Quercus alba*, *Q. rubra*, *Carpinus caroliniana*, *Sassafras albidum*, and *Cornus florida*, along with scattered individuals of *Quercus macrocarpa*, *Prunus serotina*, *Juglans nigra*, *Hamamelis virginiana*, *Cornus foemina*, *Sambucus canadensis*, *Ribes americanum*, and *R. cynosbati*. The forest ground cover is comprised of species such as *Carex gracillima*, *Festuca subverticillata*, *Milium effusum*, *Hylodesmum nudiflorum*, *Toxicodendron radicans*, and *Lysimachia lanceolata*. However, along the streambank there is a higher concentration of wet woodland species, including *Lindera benzoin*, *Angelica atropurpurea*, *Symplocarpus foetidus*, *Iris virginica*, *Packera aurea*, *Onoclea sensibilis*, *Osmundastrum cinnamomeum*, and nine species of *Carex*. The higher proportion of wetland species is understandable when one considers that the stream, with its floodplain, connects two larger wetland ecosystems.

Dry Woods (42° 53.930'N, 85° 21.379'W)

Dry Woods (C in Figure 2) best fits the dry southern forest community type. A total of 85 species, 88.2% (75 species) of which are native, were found at this site. The Total FQI is 34.1, and the Native FQI is 36.5; when the Adjusted FQI of 39.5 is taken into account, this site can be ranked as a high-quality site, of floristic importance to the state. Interestingly, the dry southern forest located in the B. D. White Preserve just on the north side of 36th Street ca. 0.5 miles away has similar FQA metrics, with 109 species (89.0% native), with a Total FQI of 37.6, a Native FQI of 40.4 and an Adjusted FQI of 38.7 (Stockdale et al. 2019).

The dry hillside habitat of Dry Woods is dominated by *Quercus velutina*, *Q. alba*, and *Q. rubra*, with scattered individuals of *Sassafras albidum*, *Hamamelis virginiana*, *Juglans nigra*, *Juglans cinerea*, *Juniperus virginiana*, *Acer rubrum*, and *Elaeagnus umbellata*. The understory is very open; sandy soils contribute to sparse ground cover (likely exacerbated by deer browsing), with only scattered species such as *Hypericum perforatum*, *Hylodesmum nudiflorum*, *Galium aparine*, *Eurybia macrophylla*, and *Dryopteris carthusiana*. A number of scattered graminoids also occur, including several grasses: *Brachyelytrum aristosum*, *Dichanthelium depauperatum*, *D. implicatum*, *D. columbianum*, *Elymus hystrix*, *Festuca subverticillata*, and several sedges, among which are: *Carex pensylvanica*, *C. blanda*, *C. gracillima*, *C. granularis*, *C. rosea*, and *C. swanii*. There is also a somewhat moist depression here where *Apocynum androsaemifolium*, *Phryma leptostachya*, and other species are found. Among the more notable

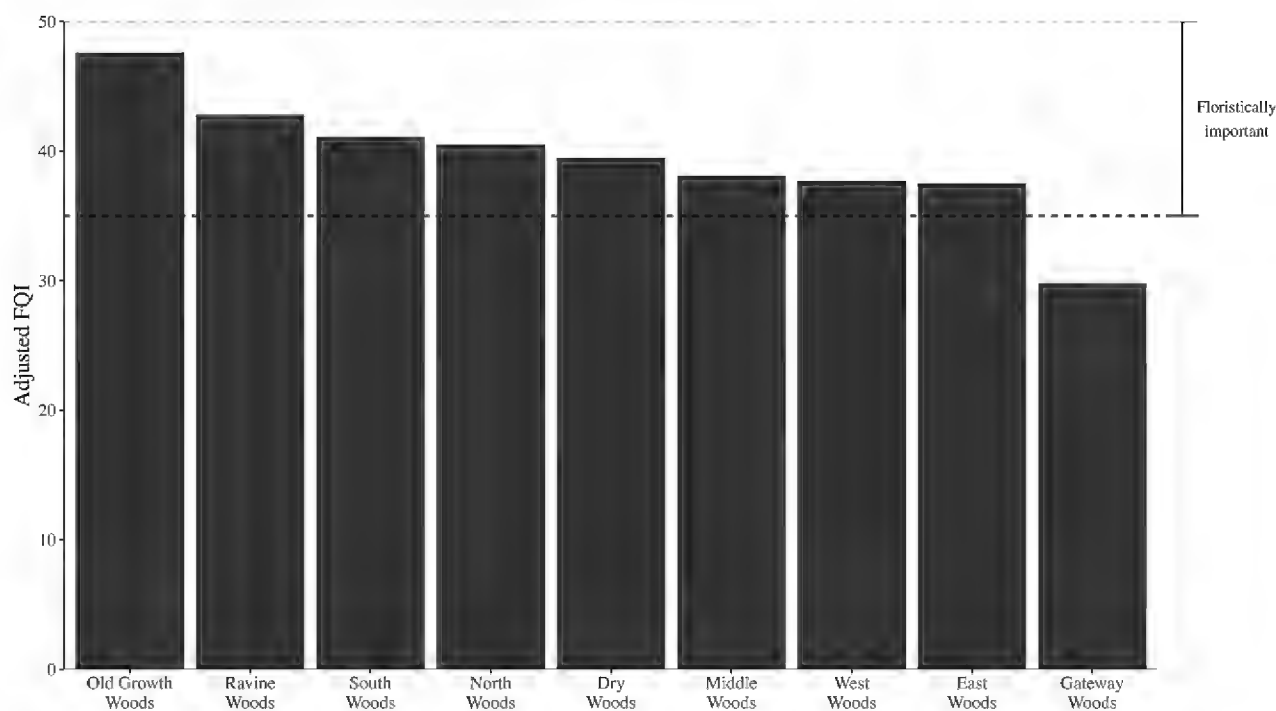


FIGURE 4. Comparison of the nine woodland study sites based on the Adjusted Floristic Quality Index (Adjusted FQI), indicating those of statewide floristic significance.

plants found in Dry Woods are *Chimaphila umbellata* and *Conopholis americana*. Two deer stands were also observed, and a herd of about 15 deer were seen at this site in spring 2019.

The outline of the Dry Woods site forms a “C” shape on a sandy hillside around a disturbed young forest on the east side of the hill (which was not inventoried). The north side of this parcel abuts North Woods, a dry-mesic southern forest that follows the stream at the bottom of the incline. The western side slopes steeply down to the large wetland of southern shrub-carr in West Wetland (WW in Figure 2). Southward is a fairly large, young, highly-disturbed secondary forest, which was not inventoried.

Ravine Woods (42° 53.821'N, 85° 21.047'W)

Ravine Woods (D in Figure 2) is wetter than most of the other wooded sites and was classified as mesic southern forest. A total of 92 species, 87 (94.6%) of which are native, were cataloged. It has the second highest Total FQI (39.3) among the nine sites, a Native FQI of 41.0, and an Adjusted FQI of 42.8 (Figure 4). It's Mean *C* value of 4.1 was the second highest of the wooded sites studied. Thus, this high-quality site is also floristically important on a state-wide basis.

Ravine Woods consists of a steep-sided stream that flows west, then north-west, into East Wetland. There are several seeps and flat areas along the top of the slope. This wooded area is characterized by *Acer saccharum*, *A. rubrum*, *Fagus grandifolia*, and *Tilia americana*, with notable scattered individuals of *Liriodendron tulipifera*, *Quercus bicolor*, *Celtis occidentalis*, *Ostrya virginiana*, and *Acer nigrum*. Three viny species, *Toxicodendron radicans*, *Vitis riparia*, and *Parthenocissus quinquefolia*, are also present. The herbaceous ground cover of the woods is indicative of a rich, moist forest and is characterized by *Geranium*

maculatum, *Podophyllum peltatum*, *Carex pedunculata*, *Solidago flexicaulis*, *S. caesia*, *Phlox divaricata*, *Hydrophyllum appendiculatum*, *H. canadense*, *H. virginianum*, *Ranunculus recurvatus*, *R. abortivus*, *Trillium grandiflorum*, *Cryptotaenia canadensis*, *Geum canadense*, and *Polystichum acrostichoides*. Along the stream bank there are species such as *Laportea canadensis* and *Asarum canadense*. In the seep areas there are additional species such as *Symplocarpus foetidus* and, notably, *Carex prasina*, along with several other more common species of *Carex*. This ravine site is bounded by agricultural lands on the north-east, east and south, and on the west by immature disturbed forest.

Old Growth Woods (42° 53.805'N, 85° 21.405'W)

Old Growth Woods (E in Figure 2) best fits a mesic southern forest plant community type. A relatively low total of 52 species was identified here, but with a very high percentage of native species, 94.2% (49 species). The aspect of this forest is impressive, with many stately trees located on a very steep north-facing slope descending into the upper reaches of the large West Wetland. On a class field trip, D. Warners had students randomly measure 80 trees in this parcel. More than half were larger than 2 feet dbh, six were greater than 3 feet dbh, and the three largest trees were a 40-inch dbh *Fagus grandifolia* (American Beech), a 46-inch dbh *Liriodendron tulipifera* (Tulip Tree), and a 48-inch dbh *Quercus rubra* (Red Oak). The Total FQI is 33.2, and the Native FQI is 34.3. Since the number of species in this wooded slope is low, the Adjusted FQI of 47.6 is the most reliable measure to affirm its value as a high-quality site, worthy of floristic recognition at the state level (Figure 4). This is further confirmed by having the highest Mean *C* value (4.6) of all the wooded sites.

As a community, this forest is dominated by *Acer saccharum*, *Fagus grandifolia*, and *Liriodendron tulipifera*, with scattered trees of *Acer nigrum*, *A. rubrum*, *Fraxinus pennsylvanica*, *Hamamelis virginiana*, *Prunus serotina*, *Tilia americana*, and *Quercus rubra*. The understory is patchy, with a species assemblage indicative of a rich woodland, with *Actaea pachypoda*, *Adiantum pedatum*, *Polystichum acrostichoides*, *Cardamine douglassii*, *Caulophyllum thalictroides*, *Collinsonia canadensis*, *Circaea canadensis*, *Euonymus obovatus*, *Hydrophyllum canadense*, *H. virginianum*, *Podophyllum peltatum*, *Sanguinaria canadensis*, *Laportea canadensis*, *Viola canadensis*, *Conopholis americana*, *Allium tricoccum*, and *A. burdickii*. Several sedges that are found here are also indicative of high-quality rich woods, including *Carex albursina*, *C. gracillima*, *C. jamesii*, *C. laxiflora*, and *C. rosea*. It is suspected that this is a remnant of old growth forest that was never logged due to its location on such a steeply sloped contour.

To the south and southeast is a successional old agricultural field shifting to meadow, part of which has been managed for prairie restoration. The east boundary is a ravine that channels runoff from the meadow. The north boundary is the large shrub-dominated wetland (West Wetland), and a large seep dominated by *Laportea canadensis* and *Symplocarpus foetidus*. Toward the west boundary there is a shift in ground cover vegetation from spring ephemerals and ferns to soils dominated by *Parthenocissus quinquefolia*; the trees are mature in this area but do not have the distinctive appearance of old growth.

Middle Woods (42° 53.705'N, 85° 21.522'W)

Middle Woods (F in Figure 2) best fits the mesic southern forest category. A total of 66 species, 90.9% (60 species) of which are native, were documented here. While the Total FQI (29.2) and Native FQI (31.0) might suggest this to be a more average quality site, the Adjusted FQI (38.1) which corrects for low species richness, is substantially higher. The Mean *C* value of 3.6 also indicates that this woods should be regarded as a high-quality mesic southern forest (Figure 4).

This parcel is dominated by *Acer saccharum* and *Tilia americana*, with less abundant woody species including *Quercus rubra*, *Carya cordiformis*, *Carya glabra*, *Celtis occidentalis*, *Fagus grandifolia*, *Fraxinus pennsylvanica*, *Juglans nigra*, *Liriodendron tulipifera*, *Acer nigrum*, *A. rubrum*, *Prunus serotina*, *P. virginiana*, *Zanthoxylum americanum*, *Carpinus caroliniana*, and *Ostrya virginiana*. The understory is heavily populated by the vines *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis riparia*, interspersed with several large colonies of *Podophyllum peltatum*. Many of herbaceous species indicative of high-quality mesic woods are found here, including *Actaea pachypoda*, *Allium tricoccum*, *Arisaema triphyllum*, *Circaea canadensis*, *Geranium maculatum*, *Hydrophyllum appendiculatum*, and *Solidago caesia*.

A small open pool habitat occurs at the interface with the prairie restoration site, dominated by an almost solid growth of *Cephalanthus occidentalis* (But-tonbush) with sparse presence of *Acer saccharinum* (Silver Maple). Because of its edge location and small size, this microhabitat was not included in the inventory.

West Woods (42° 53.732'N, 85° 21.777'W)

We classified the West Woods (G in Figure 2) as mesic southern forest. A total of 73 species, 89.0% (65 species) of which are native, were found in this ravine-dominated parcel. Once again, although the Total FQI (30.8) and Native FQI (32.2), might suggest this to be a site of only moderate conservation value, the Adjusted FQI (37.7), along with a relatively high Mean *C* value of 3.6 boosts this woods to rank with the other mesic southern forest woods as a high-quality natural area (Figure 4).

The ravine running from the cultivated field to the south delineates the woods into a southwest side and a northeast side. The southwest side is dominated by *Acer saccharum*. The northeast side is more diverse and appears to be less disturbed. It is comprised of a relatively even mix of canopy species that include *Acer saccharum*, *A. rubrum*, *Tilia americana*, *Celtis occidentalis*, *Quercus alba*, *Q. rubra*, and scattered *Fagus grandifolia*, *Fraxinus pennsylvanica*, *Juglans cinerea*, *Prunus serotina*, *Ulmus rubra*, and *Liriodendron tulipifera*. Among the more abundant herbaceous species present in the open understory are *Trillium grandiflorum*, *Hepatica americana*, *Geranium maculatum*, *Maianthemum racemosum*, *Podophyllum peltatum*, *Monotropa uniflora*, *Osmorhiza longistylis*, *Hylodesmum glutinosum*, *Dioscorea villosa*, *Onoclea sensibilis*, *Asplenium platyneuron*, and *Lindera benzoin*. Two woodland species, *Solidago caesia* and *Eurybia macrophylla*, add to the fall-flowering flora. Graminoids in this wooded site include: *Carex swanii*, *C. albursina*, *C. blanda*, *C. rosea*, *C. pennsylvanica*,

Brachyelytrum erectum, *Elymus hystrix*, and *E. villosus*.

Although much of the woods is populated by native vines such as *Vitis riparia*, *Toxicodendron radicans*, and *Parthenocissus quinquefolia*, the flora along the northwest side on a little wooded peninsula has a distinctly increased presence of weedy plants (both non-native species and adventive natives) that are usually associated with more disturbed sites, including *Rosa multiflora*, *Rubus allegheniensis*, *Phytolacca americana*, *Solidago canadensis*, and *Hesperis matronalis*, as well as a species that has recently been spreading aggressively in Michigan, *Vincetoxicum nigrum*. This rather abrupt change in flora likely indicates some type of past direct disturbance in this portion of the forest. A native species of note in this disturbed area, though, is *Campanulastrum americanum*, which occurs only occasionally in Kent County, and is never abundant.

East Woods (42° 53.600'N, 85° 21.000'W)

East Woods (H in Figure 2), which is somewhat disjunct from the other wooded sites, also best fits a mesic southern forest designation. A total of 90 species, 92.2% (83 species) of which are native, were found in this parcel. Similar to West Woods described above, the somewhat modest Total FQI of 31.4 and Native FQI of 32.4 suggest a floristically average site. However, as seen with other woods in this study, when the Total Mean *C* value (3.6) is considered with the Adjusted FQI (37.5) this parcel also ranks with the other mesic southern forest tracts as a high-quality woodland (Figure 4).

A small ravine system characterizes this forest, with a notable streamlet and floodplain, flowing northeast toward a *Cornus* thicket not considered part of this wooded site. The parcel is dominated by *Acer saccharum* and *Tilia americana*, with scattered individuals of *Acer nigrum*, *A. rubrum*, *A. saccharinum*, *Fraxinus pennsylvanica*, *Juglans cinerea*, *J. nigra*, *Liriodendron tulipifera*, *Prunus serotina*, *Quercus alba*, *Q. velutina*, *Ulmus rubra*, and *Ostrya virginiana*. The understory is characterized by the woody vines *Toxicodendron radicans* and *Parthenocissus quinquefolia*, and an herbaceous ground cover flora including such species as *Impatiens capensis*, *Arisaema triphyllum*, *Circaea canadensis*, *Dicentra cucullaria*, *Eurybia macrophylla*, *Geranium maculatum*, *Hydrophyllum canadense*, *Podophyllum peltatum*, *Symphyotrichum lateriflorum* and *Solidago caesia*. This site is also particularly rich in woodland sedges: *Carex albursina*, *C. crinita*, *C. grisea*, *C. hirtifolia*, *C. hitchcockiana*, *C. jamesii*, and *C. rosea*, as well as others that are more characteristic of wetlands such as *C. lupulina*, *C. stricta*, and *C. vulpinoidea*. The floodplain also has a population of the rare *Carex davisii*, which is listed in Michigan as Special Concern status (Michigan Natural Features Inventory 2009).

On the northwestern side of the woodland, we encountered a small vernal pool near the interface with the prairie restoration site. This transitional wet woods added 15 species to the overall flora, but these were not incorporated into the Sørensen Index of Similarity assessment because they are not typical of mesic southern forests. The pool was dominated by the amphibious *Persicaria amphibia*, with localized patches of *Matteuccia struthiopteris*, *Pilea pumila*, and *Leersia oryzoides* around the margin. A nice population of the rare *Carex davisii*

(Special Concern status) was located here, as well as elsewhere in the East Woods.

This wooded site has a notable open understory with few shrubby species and is rather isolated from the rest of the wooded areas in the Lowell Regional Greenspace. However, use of this tract historically as a dumping ground is evidenced by the presence of waste items and trash.

South Woods (42° 53.523'N, 85° 21.450'W)

South Woods (I in Figure 2) was classified as mesic southern forest. A total of 58 species, 91.4% (53 species) of which are native, were found in this site. The Total FQI of 30.5 and Native FQI of 31.3 suggest that the floristic value of this site is average, but the Adjusted FQI of 41.1 increases its rank to be comparable with the other mesic southern forest sites as a floristically high-quality site (Figure 4); this is further supported by the rather high Mean *C* value of 4.0.

This is a rather homogeneous woods dominated by *Fagus grandifolia* and *Acer saccharum* with scattered individuals of *Carya cordiformis*, *Fraxinus pennsylvanica*, *Juglans nigra*, *Prunus serotina*, *Sassafras albidum*, *Tilia americana*, *Ulmus rubra*, and the understory trees *Amelanchier laevis*, *Zanthoxylum americanum*, *Staphylea trifolia*, and *Ostrya virginiana*. The nearly ubiquitous vines *Parthenocissus quinquefolia* and *Toxicodendron radicans* are present as well. The understory herbaceous layer is rich in spring flora, characterized by *Erythronium americanum*, *Agrimonia gryposepala*, *Arisaema triphyllum*, *Sanguinaria canadensis*, *Cardamine bulbosa*, *Cardamine concatenata*, *Claytonia virginiana*, *Floerkea proserpinacoides*, *Dicentra cucullaria*, *Phlox divaricata*, *Trillium grandiflorum*, and *Podophyllum peltatum*, as well as the fern *Polystichum acrostichoides*. The sedge flora is well represented by *Carex albursina*, *C. gracillima*, *Carex jamesii*, *C. laxiflora*, *C. pensylvanica*, *C. rosea*, and *C. sparganioides*. *Solidago caesia* is notable as well. There is a surprising lack of mature maple trees found in this woodland parcel. There are, though, some remnant stumps which give evidence that selective logging likely occurred in these woods sometime in the past.

Non-metric Multidimensional Ordination (NMDS)

The NMDS ordination (Figure 3) shows that six of the woodlots (not including North Woods, Dry Woods, and Gateway Woods) cluster together and therefore, based on presence/absence data, are most similar to each other. The Gateway Woods and Dry Woods are positioned relatively close to one another in similarity as well, but distanced from the rest. The North Woods is set apart in this analysis, indicating that it is clearly the most dissimilar of the wooded parcels, exhibiting an assemblage of vegetation with the least amount of overlap to the other patches. The stress value of this ordination is 0.0455, indicating a very good fit.

The results of the NMDS confirm that the dry areas (Gateway Woods and Dry Woods) form similar communities while the other mesic woods form a different community type. The uniqueness that the North Woods experiences as a low riparian forest between East Wetland and West Wetland, both fitting the shrub-carr

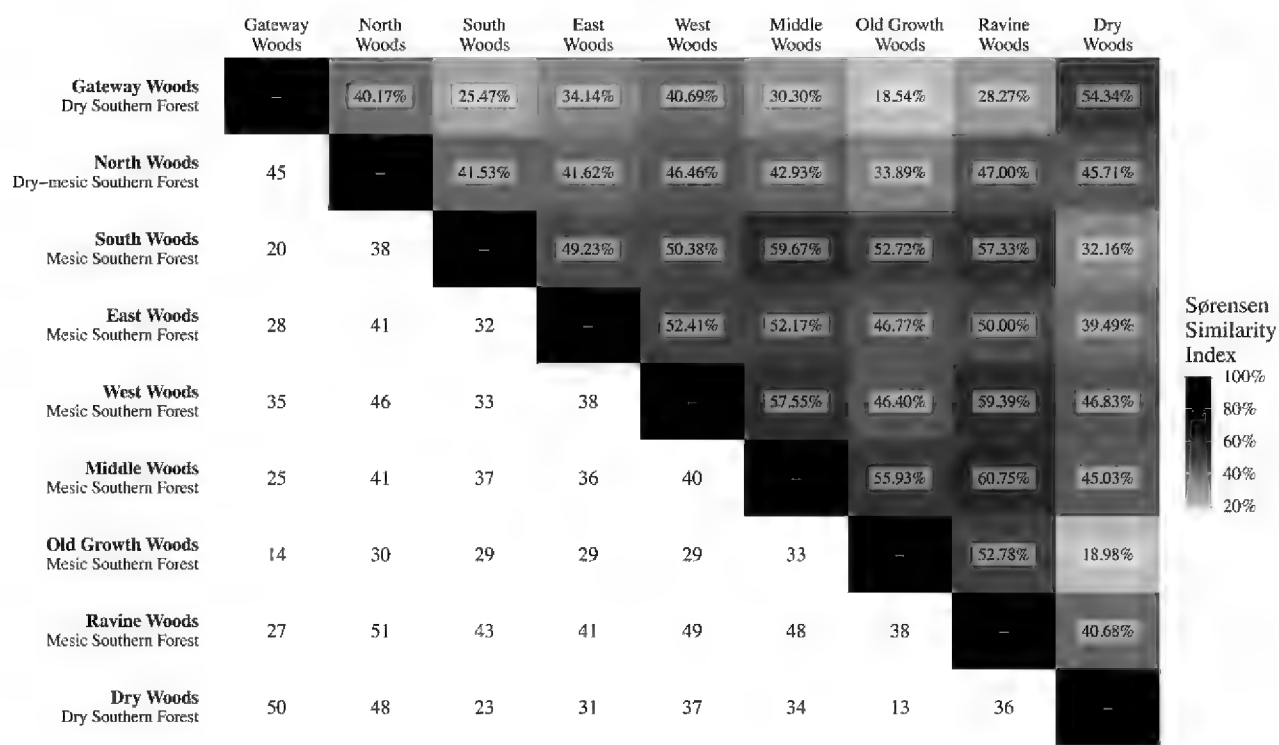


FIGURE 5. Sørensen Index of Similarity for each pair of the nine woodland sites. Values in the shaded boxes to the upper right of the diagonal are the percentage similarity of each pair; values to the lower left of the diagonal are the number of species shared between pairs of woodland sites. The forest classification of each site is indicated in the left column under the name of that site.

community type, is evident in its high species richness and the uniqueness of the species present. Also notable is the distance between the Old Growth Forest and Gateway Woods, the two sites lying furthest from each other on the ordination. Gateway Woods, which shows evidence of significant historical disturbance, is the most different from the nearly pristine Old Growth Woods, compared to all other possibilities.

Similarity Index

Initially, the collection of woodland sites at the Lowell Regional Greenspace appeared to be rather similar, and, in attempting to apply the Michigan Natural Features Inventory’s (MNFI) natural communities classification system (Cohen et al. 2015), we were inclined to assign them to a single habitat type. The non-metric multidimensional ordination confirmed that several of the wooded sites cluster rather close. Recognizing that plant communities often exhibit a continuum of variability, we also employed the Sørensen Index of Similarity to assess how similar these various woodlots are floristically. Two sites can be considered to be essentially the same type of plant community, in the sense of Curtis (1959), when they exhibit a Similarity Index score greater than 50% (Curtis 1959; Bradley and Crow 2010).

Four of the sites—East Woods, West Woods, Middle Woods, and Ravine Woods—had a Sørensen Index score in the 50.0–60.75% range for all pairwise comparisons (Figure 5). Additionally, South Woods showed a very strong affinity with these tracts, only slightly below the 50% threshold in its comparison

with East Woods (49.23%). Old Growth Woods showed a strong similarity with three of these sites: Middle Woods (55.93%), Ravine Woods (52.78%) and South Woods (52.72%). These results led us to conclude that all six of these woodland sites best fit the MNFI's mesic southern forest habitat type (Cohen et al. 2015).

On the other hand, two forest sites, Gateway Woods and Dry Woods, were strongly correlated with each other at 54.34%, but had low Sørensen Index scores when compared to each of the other parcels. We considered both of these tracts fit best the dry southern forest community type. North Woods alone had no comparisons with any of the other sites that met the 50% threshold, and we therefore treated this parcel as a separate forest type—dry-mesic southern forest.

Rare Plants

Three species with rarity status in the State of Michigan (Michigan Natural Features Inventory 2009) were discovered in the Lowell Regional Greenspace, but because of the sensitivity of any Threatened or Endangered state-listed plants, we have withheld specific locality data.

Hydrastis canadensis: Threatened status. MICHIGAN FLORA ONLINE (2011) indicates that this rare species is a plant of rich deciduous forests. Although this database documents 81 specimens from 19 counties in southern Michigan, many of them are old collections. Emma Cole (1901) regarded this species as “scarce,” with only a few plants at any station, but otherwise well-distributed within the greater Grand Rapids area. Our site fits Cole’s description of local, with few plants. This appears to be the first specimen documenting *Hydrastis canadensis* from Kent County since the late 1890s. Voucher: *Walt & Hartwig EC-19-4347* (CALVIN, MICH).

Carex davisii: Special Concern status. This is a handsome cespitose sedge typically of floodplain forests, which in Michigan occurs only in 11 counties, all in the southern portion of the state. This sedge was found to be locally abundant only in East Woods, nearby to where the creek flows into a small floodplain-like site dominated by Silver Maple (*Acer saccharinum*) and Buttonbush (*Cephalanthus occidentalis*). Voucher: *Walt & Hartwig EC-19-3922* (CALVIN, MICH). *Carex davisii* was earlier reported from Kent County at one of Emma Cole’s favorite collecting sites (Cole 1901), the Lamberton Creek mouth at Soldier’s Home Woods (Stockdale et al. 2019). We have also collected vouchers of this species at Grand Ravines Park, Ottawa County, *Antuma & Murphy EC-17-1744* (CALVIN, MICH); *Antuma & Van Donselaar EC-17-1914* (CALVIN, MSC); and Grand River Park, Ottawa County, *Van Donselaar, Antuma & Quakenbush EC-17-2187* (CALVIN, MICH).

Lithospermum latifolium: Special Concern status. This rather unassuming herb was found in Dry Woods, growing in a small depression; only two plants were present. Voucher: *Walt & Hartwig EC-19-4304* (CALVIN). We have also collected vouchers of this species at Ken-o-Sha Park, City of Grand Rapids, *Leisman, Van Staalduinen, & Warners EC-15-379* (CALVIN), at Mr. Lowes’ Woods, Ball-Perkins Park, City of Grand Rapids, *Crow 11190* (CALVIN, MICH) (Stockdale et al. 2019), and at Hilbrands Property, Cascade Township, Kent Co., *Antuma & Quakenbush EC-17-1623* (CALVIN, MICH, MSC).

CONCLUSION

This study evaluated nine mature forest parcels that co-exist within a limited geographic area and are all relatively similar in size (ranging from 2.56–7.65 ha; with Gateway Woods much smaller at 0.49 ha) (Table 1). In viewing the proposed Lowell Regional Greenspace via Google Earth (Figure 2), the forest community at this location appears to be fairly expansive, but field-based observations reveal that much of the wooded landscape consists of young, early- to mid-successional woodlands rather than mature forest. Given the size of the trees, multi-aged forest composition, and overall community structure, the parcels that we determined to be high-value woodland tracts are likely vestiges of the old farm woodlot type. Although floristically dynamic over time, these remnant habitats have retained much of their presettlement forest character.

In an analysis of change over a period of 40 years in a high-quality Michigan woods, Kolp et al. (2021) documented a net loss of native species while gaining in overall diversity by the addition of non-native species, an overall change in diversity of 3%. Yet, interestingly, they also documented a total of 28 native species (five with high *C*-values of 8–10) that were newly recruited within this 40-year period. It is noteworthy that a lack of connectivity with other natural areas is an important factor that can hinder the recruitment of native species migrating into other woodlands (Brudvig et al. 2009). We propose that after clear-cutting at the Lowell site for agricultural purposes that occurred in the mid-19th century, these high-quality woodland parcels have been functioning as refugia, providing propagule sources for many native woodland plants to spread as the process of change from agricultural land toward successional woodlands has more recently been occurring. This process is no doubt continuing today, albeit possibly hindered by the counteracting influence of non-native invasive plants and a preponderance of deer.

We found remarkable differences among the nine woodlots situated within this Lowell Regional Greenspace. Old Growth Woods (E in Figure 2) has the highest natural quality with an Adjusted FQI of 47.6 (Figure 4) and highest Mean *C* (4.6). When visited, this forest displays an exceptional visual impression with its high canopy, carpet of spring wildflowers, diversity of large trees, and overall open aspect. This site has a look and feel that is unique among these nine parcels, owing to the minimal amount of disturbance that has occurred here over time because of its steeply sloped aspect. Ravine Woods, South Woods, and North Woods are similarly noteworthy for their conservation value with an Adjusted FQI for each that is over 40 (Figure 4). Yet these parcels appear to have experienced more disturbance over the years than Old Growth Woods. We strongly recommend to Kent County Parks that only passive recreational activities be permitted in these four woodlots as they continue plans toward developing the Greenspace. Additionally, we encourage vigilant monitoring and management for encroaching invasive species in these locations.

A close assessment of species composition across all nine sites (Table 1) further illuminates the variability among these parcels, even among those that scored high on the Sørensen Index of Similarity. In fact, of the 241 total native

woodland species identified in this study, 90 of them (37% of the total) occur in only one of the nine woodlots. This distribution highlights the differences between the remnant forest patches, and also suggests that these native species are vulnerable to local extinction. The dedicated effort of Kent County Parks to secure this land for preservation and public use is a welcome and hopeful step forward in stemming the tide of native species loss that has paralleled the expanding land development patterns in West Michigan.

The two forest sites exhibiting greatest dissimilarity according to the Sørensen Index were Old Growth Woods and Dry Woods (Figure 5). These two tracts were only found to be 19% similar even though they are located directly across from each other, separated only by a narrow lobe of the West Wetland (Figure 2). Having two mature forest stands located so close to each other, yet sharing only 13 species in common illustrates how markedly forest composition can shift within a small spatial scale. Such high-diversity in a limited space underscores the importance of preserving as many remaining remnant habitats as possible (Whittaker 1960; Tuomisto 2010).

Even though the forest parcels in this study are relatively small, they retain significant native plant diversity, collectively harboring a total of 274 species, with 241 (88%) being native. While conservation efforts across North America tend to prioritize large patches of land for protection, this study shows that small parcels such as farm family woodlots should not be overlooked. E. O. Wilson has emphasized that, “. . . every scrap of biological diversity is priceless, to be learned and cherished, and never to be surrendered without a struggle” (Wilson 1992). In some ways these former farm woodlots are examples of Wilson’s “scraps” of biodiversity. And by preserving them, we allow possible connections to emerge, both physically—by offering dispersal opportunities into regenerating secondary forests—and genetically—through shared pollination and seed dispersal activities. In these ways, old leftover farm woodlots can serve as inoculation sources for expanding native Michigan forest communities into the future.

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MOLECULAR DATA REVEAL THE SECRET MEETING OF THE AMERICAN AND EASTERN BEAKED HAZELNUTS

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ABSTRACT

The patterns of biological diversity in various parts of the Earth may have resulted from speciation, extinction, and geographic migration, and understanding the mechanisms of the formation of the various patterns is important for sensible stewardship of biological diversity. *Corylus* L. (Hazel-nut) is a plant genus of 14–19 species with a disjunct distribution between Eurasia and North America. While most species of *Corylus* are distributed in the Old World, three taxa, consisting either of (i) three species or (ii) two species, one of which has two subspecies, are endemic to the New World. In this study, multiple nuclear genes and complete plastomes were gathered using high throughput sequencing technology and analyzed using maximum parsimony, Bayesian, and multi-species coalescent methods to gain a better understanding of the phylogenetic and biogeographic relationships of the North American species. Our results suggest that *Corylus americana* Walter, *C. cornuta* Marshall, and *C. californica* (A. de Candolle) Rose (more recently recognized as a subspecies of *C. cornuta*) represent separately evolving lineages in North America as shown by the nuclear genes, while *C. americana* and *C. cornuta* demonstrated the admixture of plastomes with each other but not with *C. californica*. Therefore, the molecular data revealed the geographic meeting of the two eastern North America species after the separation of *C. cornuta* in the east and *C. californica* in the west.

KEYWORDS: hybridization, hazelnuts, plastome, angiosperm353 probes, biogeography

INTRODUCTION

Understanding the differential distribution and diversity of organisms has been a core task for ecologists and biogeographers, and may provide potential solutions to solving many urgent issues that humans face (Gaston 2000). The patterns of biodiversity can be seen at different geographic scales from the entire globe to a local ecosystem, and in various taxonomic levels from global flora and fauna to a single genus or species (Li et al. 2018).

Corylus L., commonly known as hazelnut or filbert, is a disjunct genus between the Old and New Worlds (Li 1952; Boufford and Spongberg 1983; Hong 1993; Wen 1999), with three taxa in North America, one species in Europe, two species in both Europe and western Asia, and 10–15 species in eastern Asia. Species of *Corylus* differ in growth habit (tree versus shrub), leaf shape, type and

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density of trichomes, involucre (bracts surrounding the ovaries) morphology, relative length of the petiole and blade, food quality, and disease resistance (Hummer 1995; Whitcher and Wen 2001). Within *Corylus*, two or three major divisions (sections or subgenera) have been recognized by some authors based on the morphology of the involucre. Subgenus or section *Acanthochlamys* is characterized by the spiny involucre (Spach 1841; de Candolle 1864; Schneider 1916; Bobrov 1936; Li and Cheng 1979; Whitcher and Wen 2001), while the remaining species have either tubular or leafy involucre and have been treated as a single section with two (de Candolle 1864; Schneider 1916; Li and Cheng 1979) or three (Whitcher 1999) subsections, two sections (Spach 1841), or two subgenera (Bobrov 1936). Molecular phylogenetic studies based on nuclear ribosomal DNA sequence data (Forest et al. 2000; Whitcher and Wen 2001) and whole genome single nucleotide polymorphisms (SNP) (Yang et al. 2018a) supported the circumscription of the subgenera or sections.

In North America, there are three taxa in *Corylus*: *C. americana* Walter and *C. cornuta* Marshall in the east, and *C. cornuta* subsp. *californica* (A. de Candolle) E. Murray in the west (Furlow 1990, 1997). *Corylus americana* is in the subsection *Corylus* or subgenus *Phyllochlamys* with a leafy involucre, while *Corylus cornuta* Marshall is in the subsection or subgenus *Siphonochlamys* with a tubular involucre. The taxonomic placements of the species in the respective subgenera or subsections were supported by DNA sequences from nuclear genomes (Forest et al. 2000; Whitcher and Wen 2001; Yang et al. 2018a; Zhao et al. 2020). However, DNA sequences from a few chloroplast genes (Forest et al. 2000) or complete chloroplast genomes (plastomes) (Yang et al. 2018b; Zhao et al. 2020) did not support the placement of *Corylus americana* and *C. cornuta* into their respective subgenera. Instead, the two species were shown to be more closely related to each other than either was to any other species in the genus (Zhao et al. 2020). *Corylus americana* and *C. cornuta* might have diverged from each other by the early Oligocene, as estimated with the nuclear SNP (single nucleotide polymorphism) data (Yang et al. 2018a), or by the middle Miocene inferred from sequences of nrDNA ITS regions (Helmstetter et al. 2019). Unless there was hybridization and introgression causing chloroplast capture between *Corylus americana* and *C. cornuta*, we would not expect their chloroplast genomes to be more similar to each other than to other species of *Corylus*. To test the hypothesis of the shared plastome between *Corylus americana* and *C. cornuta*, we needed to obtain the whole chloroplast genomes of multiple samples of both species from locations where both species occur naturally. In Michigan, *Corylus americana* occurs mostly in the lower two-thirds of the Lower Peninsula and in four counties of the Upper Peninsula, and *C. cornuta* occurs throughout the Upper Peninsula and in the northern third to half of the Lower Peninsula (MICHIGAN FLORA ONLINE 2011); there are a few counties where both species occur. The aim of the study was to test the phylogenetic incongruence between nuclear and plastome genomes and to explore the implications of the discrepancy for the phylogenetic and biogeographic relationships of the North American hazelnuts.

TABLE 1. Sources of samples of each species used in the study and voucher specimens of each. Materials were derived from the Arnold Arboretum (AA), Pierce Cedar Creek Institute (PCCI) in Hastings, Michigan, and other wild-collected specimens. Voucher specimens are deposited in the Hope College Herbarium (HCHM) and Arnold Arboretum (A).

Species	Voucher No.	Source and Herbarium
<i>Carpinus betulus</i>	Li 6911	AA 120-74A, cultivated (A)
<i>Corylus americana</i>	Li 4301	AA 1229-A, cultivated (A)
	Li 7000	PCCI, Hastings, Michigan (HCHM)
	Li 7004	PCCI, Hastings, Michigan (HCHM)
	Li 7059	Ingham Co., Michigan (HCHM)
	Li 7060	Ottawa Co., Michigan (HCHM)
	Li 7063	Middleville, Michigan (HCHM)
	Li 6823	Lewis Co., Washington (HCHM)
<i>Corylus californica</i>	Li 6830	Washington Co., Oregon (HCHM)
	Li 6833	Lane Co., Oregon (HCHM)
	Li 6860	Lane Co., Oregon (HCHM)
	Li 6883	New York (HCHM)
<i>Corylus cornuta</i>	Li 7005	Mason, Michigan (HCHM)
	Li 7008	Mason, Michigan (HCHM)
	Li 7012	Mason, Michigan (HCHM)
<i>Corylus wangii</i>	Li 6817	Rongjing Sichuan (A)
<i>Corylus yunnanensis</i>	Li 6820	Muli, Sichuan (A)

MATERIALS AND METHODS

Seventeen plant samples were used in this study, representing *Corylus americana*, *C. cornuta*, *C. cornuta* subsp. *californica*, and the outgroup *Carpinus betulus* L., *Corylus wangii*, and *C. yunnanensis* (Table 1). Because previous phylogenetic analyses using plastome sequence data (Yang et al. 2018b) indicated that species of *Corylus* formed a clade and the earliest sequences were from *Corylus wangii* and *C. yunnanensis* (Franch.) A. Camus, we used the latter species as outgroups to root the plastome trees of the North American species. In the nuclear gene trees, *Carpinus* L. was included to root the trees, since the relationships among the major lineages of *Corylus* differ among the recent analyses (Yang et al. 2018a; Helmstetter et al. 2019; Zhao et al. 2020).

The genomic DNAs were extracted using the OPS Diagnostics DNA Purification kit (Lebanon, New Jersey). Genomic libraries of 353 targeted nuclear loci were constructed, enriched, and sequenced at the ArborBiosciences Company (Ann Arbor, Michigan) using the angiosperm353 probe set (Johnson et al. 2019). Sequencing reads were cleaned with the Trimmomatic program (Bolger et al. 2014) with the following options: ILLUMINACLIP: adapters/TruSeq3-PE.fa:2:30:10 LEADING:20 TRAILING:20 SLIDINGWINDOW:4:20 MINLEN:50. Exons were extracted from the cleaned reads using the HybPiper package (Johnson et al. 2016) on the Hope College computer cluster with the angiosperm353 target sequences and the BWA assembly (Li and Durbin 2009). The extracted sequences were aligned using the MAFFT algorithm (Katoh and Standley 2013) and concatenated in the PHYLOSUITE platform (Zhang et al. 2020). The nuclear loci missing from one or more samples were removed from further analyses. The off-target sequencing reads were used to construct plastid genomes of the samples against the reference genome available at the GenBank (MH628454) (Yang et al. 2018b) in the Sequencher program (version 5.4.6., GeneCodes, Ann Arbor, Michigan). The plastid genomes were annotated on the online server of CHLOROBOX with the GeSeq module (Tillich et al. 2017) and *Corylus wangii* Hu as the reference (Yang et al. 2018b). Plastomes from additional samples were obtained from the GenBank (*Corylus americana*) (Yang et al. 2018b) and from the off-target reads of another nuclear probe set designed by Buddenhagen et al. (2016) (*Corylus americana*: 4301, 7060; *C. californica*: 6823, 6833; *C. wangii*: 6817, and *C. yunnanensis*: 6820). Regions of ambiguous alignment were detected and removed from further analyses using the GBLOCK algorithm (Castresana 2000; Talavera and Castresana 2007) as implemented in the PHYLOSUITE (Zhang et al. 2020).

Phylogenetic analyses were done using both the maximum parsimony (MP) and Bayesian inference (BI) methods as implemented in MEGA (Kumar et al. 2018) and MrBayes (Ronquist et al. 2012) on the CIPRES platform (Miller et al. 2010), respectively. The MP analyses were performed with the following options: heuristic search with TBR (tree bisection reconnection) method, 10 random tree addition, search level 3, and 5000 trees retained. Bootstrap analysis (Felsenstein 1985) was conducted to evaluate support for individual clades with 500 replicates and the same tree search options as in the MP analysis. For Bayesian tree inference, we performed two MCMC runs each with 10 million generations and four chains. The first 20% of the generations were discarded as burnins, and the 95% consensus trees were used for posterior probability support for the relationships.

Partitions of the nuclear loci were inferred using the PartitionFinder 2 (Lanfear et al. 2016), as implemented in the PHYLOSUITE package (Zhang et al. 2020), with the following parameters: branch lengths = linked, models = GTR, GTR+G, GTR+I+G, model selection criterion = AIC, and search scheme = hcluster. Maximum likelihood trees were estimated with the IQ-TREE program (Nguyen et al. 2015) as implemented in the PHYLOSUITE package (Zhang et al. 2020). The estimated maximum likelihood trees from individual partitions were used as input trees to infer species trees in the ASTRAL computer program that considers discordance between partitions and estimates the potential impact of the incomplete lineage sorting based on the multiple species coalescent model (Zhang et al. 2018).

RESULTS

We successfully extracted DNA sequences from 352 nuclear loci utilizing the HybPiper pipeline (Johnson et al. 2016). However, five loci (5064, 6366, 6406, 6526, and 6731) were missing from one to 10 samples and were removed from further analyses. The remaining nuclear data set is composed of 347 loci and 278,490 sites, 5186 of which were parsimony informative. The MP analysis of the combined nuclear data set generated a single most parsimonious tree with 22,387 steps, CI=0.78, and RI=0.57 (Figure 1). When rooted with *Carpinus*, two robust clades were recognized: *Corylus americana* and the clade containing *C. californica* and *C. cornuta*. The model test conducted in the PAUP* program (Swofford 2002) suggested that the optimal model for the data was the GTR+I+Gamma model. The BI trees showed a topology similar to that of the MP tree (Figure 1). The partition analysis with the PartitionFinder2 (Lanfear et al. 2016) identified 346 partitions. The multiple species coalescent-based analysis of the separate partitions generated a species tree with similar relationships as in both the MP and BI trees.

The original aligned plastome data set had 135,982 sites. After the ambiguous sites were removed in the GLOCK computer program, the final plastome data set contained 130,854 sites, 308 of which were parsimony informative. Parsimony analysis produced 20 most parsimonious trees of 621 steps, CI=0.94, and RI=0.93 (Figure 2). Samples of *Corylus californica* formed a clade with strong support (bootstrap, bs=100%), which is sister to the clade (bs=99%) containing *Corylus americana* and *C. cornuta*, whose samples did not form separate their own clades. The two clades were also strongly supported in the BI trees (pp, posterior probability=1.0) (Figure 2).

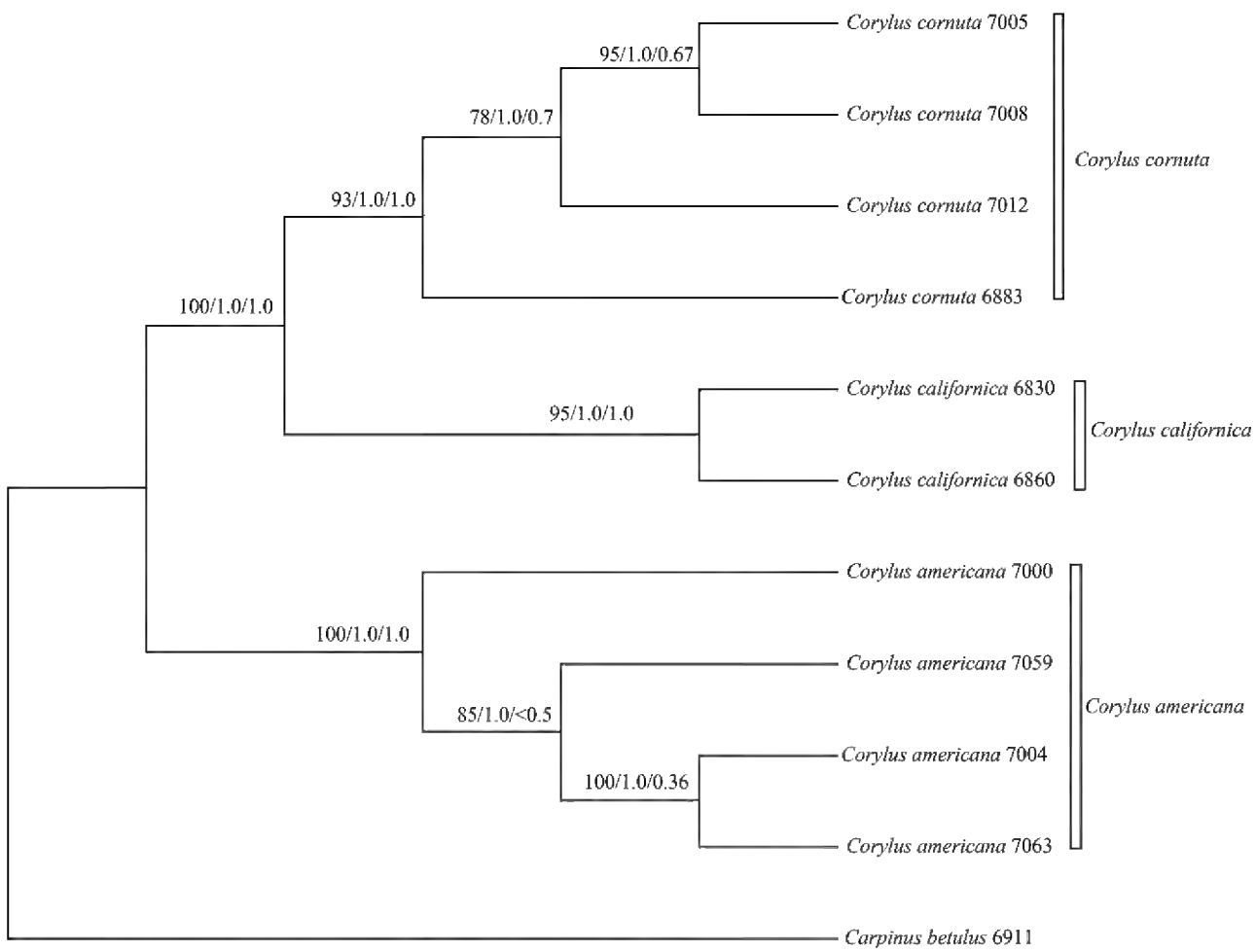


FIGURE 1. Phylogeny of North American *Corylus* produced by maximum parsimony (MP), Bayesian, and Astral analyses of the nuclear data set containing 278,490 sites. The three numbers at each of the branches are MP bootstrap percentages/Bayesian posterior probabilities/Astral support indices. Voucher numbers follow each species name.

DISCUSSION

Topological differences of nuclear and plastid trees have been reported in various plant lineages (Rieseberg et al. 1996; Zhang et al. 2010; Lin et al. 2019) including *Corylus* (Erdogan and Mehlenbacher 2000; Helmstetter et al. 2019; Zhao et al. 2020). In *Corylus*, one incongruence between nuclear and plastome trees is reflected in the phylogenetic relationship of *Corylus americana* and *C. cornuta* (Zhao et al. 2020; Figures 1 and 2). The two species differ in female structures: tubular bracts in *C. cornuta* and its close relatives such as *C. mandshurica* Maxim., and leafy bracts in *C. americana* and close relatives including *C. avellana* L. and *C. heterophylla*. The close relationships among species with the same bract morphology are supported by the nuclear SNP (single nucleotide polymorphism) (Yang et al. 2018a; Zhao et al. 2020) and orthologous gene data (Figure 1). The phylogenetic incongruence is most likely related to hybridization and introgression, and/or incomplete lineage sorting (ILS) (Wendel and Doyle 1998). However, the ILS occurs when divergence times are short and population size is large (Pamilo and Nei 1988). Because the plastome is a haploid genome and its effective population size is generally half that of the nuclear ones, the plastid genome is less likely to experience the ILS than the nuclear genome.

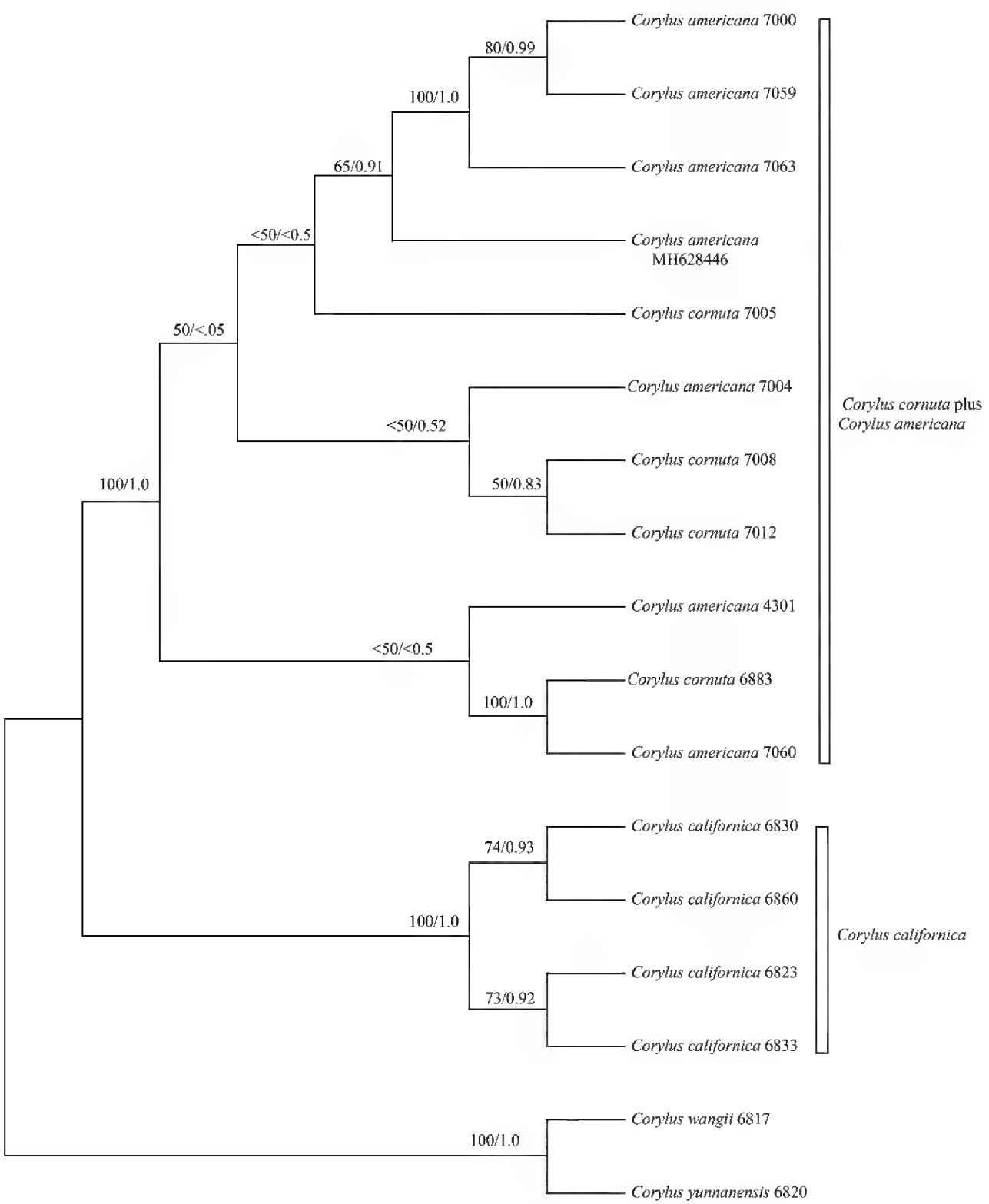


FIGURE 2. Phylogeny of North American species of *Corylus*, generated by maximum parsimony and Bayesian inference analyses of the complete plastome data set with ambiguous sites removed. 130,854 sites are included. The two numbers at each of the branches are bootstrap percentages and posterior probabilities. Voucher numbers follow each species name.

Therefore, hybridization and introgression appear to have contributed to the cytonuclear discordance in many plant groups (Folk et al. 2017; Lee-Yaw et al. 2019; Ataei et al. 2020). In both combined and partition-based phylogenies, *Corylus americana* and *C. cornuta* each form their own clades, which is indicative of little evidence of the ILS. In addition, the two lineages (*Phyllocllamys* and *Siphonochlamys*) to which the two species belong diverged by the late

Miocene (Helmstetter et al. 2019) or the early Oligocene (Yang et al. 2018a; Zhao et al. 2020). Thus, hybridization and introgression may have caused the plastome similarities between *Corylus cornuta* and *C. americana*. In North America, *Corylus californica*, a native of the Pacific coastal regions, has been recognized as a separate species (Bassil et al. 2013) or as a subspecies of *Corylus cornuta* (Furlow 1990, 1997). Both nuclear and plastome data (Yang et al. 2018a, b; Zhao et al. 2020) recognize *C. californica* as a separately evolving lineage from *C. cornuta*. In addition, morphologically *C. californica* differs from *C. cornuta* in leaf morphology, fruit size, and the tubular involucre (Furlow 1997). Our data therefore support the recognition of these taxa as distinct species, following the Gen-morph species concept (Hong 2020).

Corylus americana and *C. cornuta* in eastern North America show the admixture of the plastome as indicated by the non-monophyly of the two species (Figure 2). However, none of the sequenced individuals of *C. americana* share the plastome with *C. californica*, which suggests that the admixture of the plastome between *C. americana* and *C. cornuta* happened after the divergence of the two North American species (Figure 2). *Corylus americana* is most closely related to *C. heterophylla* Fisch. ex Trautv. in eastern Asia but diverged from the latter in the early Pliocene (Helmstetter et al. 2019) or the Middle Miocene (Yang et al. 2018a; Zhao et al. 2020). Thus, it is likely that the ancestral populations of *C. americana* emigrated into eastern North America via the Beringia land bridge. Artificial hybridization experiments conducted in three years (Erdogan and Mehlenbacher 2000) showed little success of hybridization between *C. americana* and *C. cornuta*. However, when the cross was performed with *C. cornuta* as female parent and *C. americana* as the male parent, low seed set was obtained but the percentage of survival of the seedlings was high (Erdogan and Mehlenbacher 2000). The hybridization results seem to be consistent with the chloroplast introgression from the maternal *C. cornuta* to *C. americana* when the ancestral populations of the two species met in eastern North America by the Pliocene or the Middle Miocene (Yang et al. 2018a; Helmstetter et al. 2019; Zhao et al. 2020). Although *C. americana* and *C. cornuta* differ greatly in morphology and nuclear genes, the hybridization and introgression of the plastome provides us with a clue to when and where the two species started to live side by side.

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NOTEWORTHY COLLECTION

FIRST RECORD OF THE INVASIVE MILE-A-MINUTE WEED OR ASIATIC TEARTHUMB, *PERSICARIA PERFOLIATA* (POLYGONACEAE), IN MICHIGAN

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Significance of the Report. *Persicaria perfoliata*, an invasive species on the Michigan watch list, is reported for first time in Michigan at the Whitehouse Nature Center, Calhoun County.

Previous Knowledge. *Persicaria perfoliata* (L.) H. Gross is a prickly annual vine native to eastern Asia (Oliver 1996). Since it was introduced to York County, Pennsylvania, in the 1930s, it has spread rapidly in mid-Atlantic states (University of Georgia 2021) and can potentially invade the Great Lakes states. Its presence has been confirmed in Monroe County, Indiana, and Richland County, Ohio, at locations that are about 170 and 260 km distant, respectively, from Calhoun County, Michigan (University of Georgia 2021).

Persicaria perfoliata is a species of concern. It grows rapidly in dense tangles that overtop and smother shrubs and small trees, thereby diminishing plant and wildlife diversity, forest regeneration, and horticulture. Small retrorse prickles on its stems and leaf blades make its viny thickets troublesome to navigate and manage. And its fecundity, multiple dispersal modes, and extended seed viability make it highly invasive and challenging to control (Oliver 1996; Van Clef and Stiles 2001).

Discussion. My discovery of *Persicaria perfoliata* in Albion College's Whitehouse Nature Center on October 3, 2020, was serendipitous. While searching for late-dispersing house wrens on the edge of a shrubby post-agricultural field, I saw ripening spikes of iridescent blue fruits that were new to me, despite my having worked in the Nature Center every summer since 1995 studying breeding house wrens and having studied introduced bird-dispersed fruits (White and Stiles 1992). My 2020 field season extended unusually into the fall because COVID-19 altered my teaching schedule. Despite the distinctive fruits and leaves of this species, my identification attempts with field guides and floras failed. But an Internet search for "introduced vine perfoliate" returned a perfect match posted by the National Invasive Species Information Center (USDA 2021). I then realized I had been overlooking a second vegetative patch of *P. perfoliata* in the same field all summer. These two small patches contained scores of individual annual plants, which suggested that *P. perfoliata* had become estab-

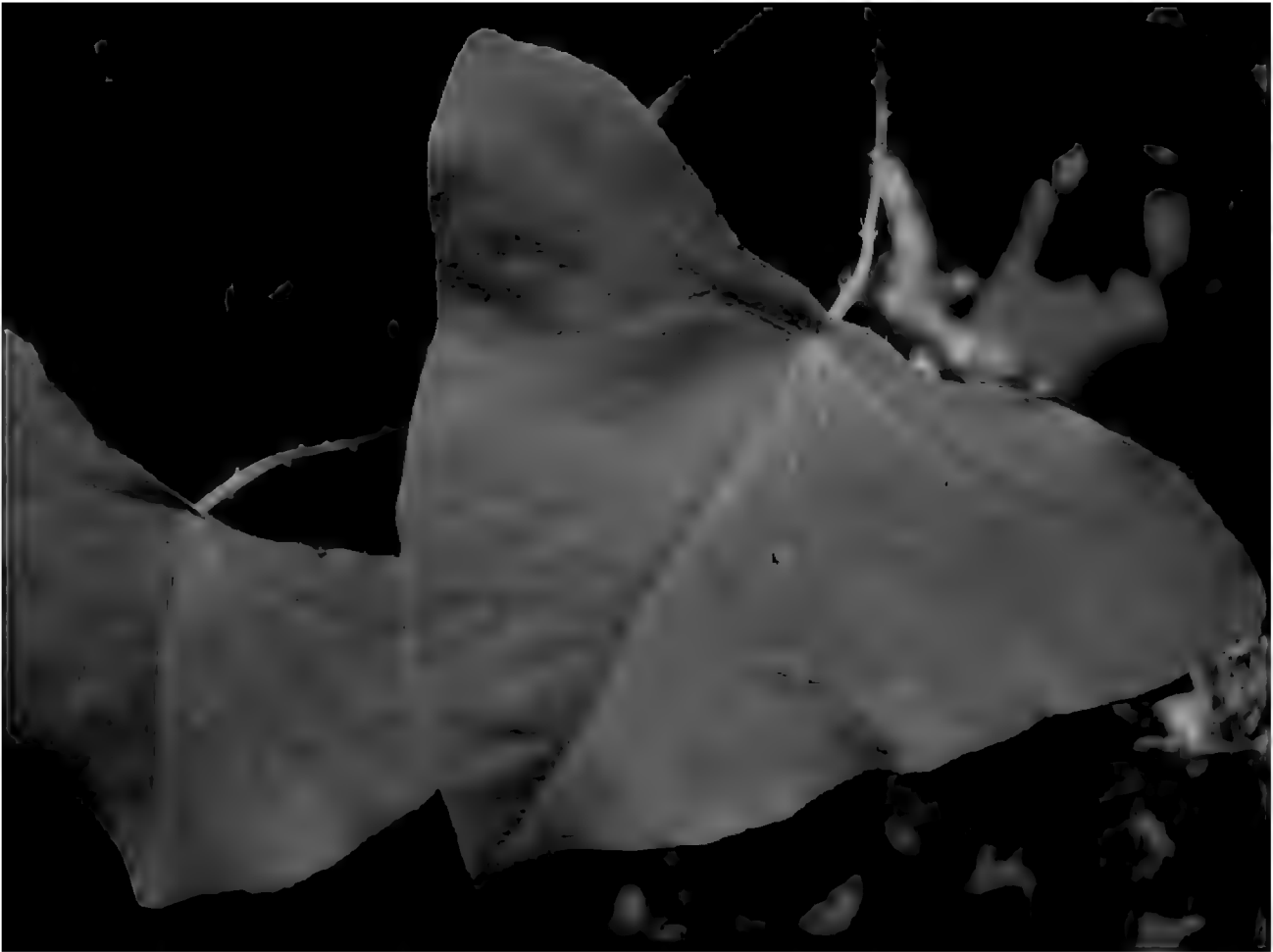


FIGURE 1. Triangular perfoliate leaves of *Persicaria perfoliata*. Whitehouse Nature Center, Albion, Michigan. Photo by Douglas W. White.

lished there before 2020. Frost kills *P. perfoliata* vines, but migratory flocks of fruit-eating cedar waxwings, gray catbirds, and American robins arrive before fall die back. Frost-shriveled fruits appear unlikely to attract fruit-eating birds. Dead vines retain withered leaves that render them visually distinctive. Thus, on November 11, 2020, I spotted a dense population of *P. perfoliata* in a 0.7 ha area of wooded wet low ground heading the Murdock agricultural drain just east of the Nature Center. *Persicaria perfoliata* may well have been established there for several years before spreading about 600 m into the Nature Center. Because this species is known to be invasive and is on the Michigan watch list (State of Michigan 2021), observations of *P. perfoliata* were reported to the Midwest Invasive Species Information Network (Michigan State University 2021). Notification triggered a coordinated response from the Michigan Department of Natural Resources, the Michigan Department of Agriculture and Rural Development, and the Cooperative Invasive Species Management Area (CISMA) authorities for Calhoun and Jackson counties. News releases were quickly distributed to local and regional media outlets revealing another Calhoun County population 7 km away. Albion College students flagged locations then removed *P. perfoliata* plants from the two Nature Center patches. In summer 2021, Barry, Calhoun, Kalamazoo CISMA contacted landowners near the Nature Center, walked their properties, and identified two more small populations. The



FIGURE 2. Hastate leaves of *Persicaria arifolia*. Indiana Dunes National Park, Porter County, Indiana. Photo by Michael Huft.

dispersal and seed dormancy adaptations of *P. perfoliata* mean that efforts to eradicate this infestation will require expanded and sustained surveillance.

Diagnostic Characters. *Persicaria perfoliata* is somewhat similar to two smaller lax sprawling native annual species that are also beset with retrorse prickles, *P. arifolia* (L.) Haraldson and *P. sagittata* (L.) H. Gross. It differs in its striking metallic blue-purple fruits and the unique circular, spreading and leaf-like ocreae that encircle the stems at the nodes making them appear perfoliate. Both *P. arifolia* and *P. sagittata* have pinkish fruits and tubular ocreae that sheath the stem. In addition, the shapes of the leaves of the three species are quite different from each other: *Persicaria perfoliata* has triangular leaves that, unlike the other two species, are perfoliate (i.e., the basal part of the leaf blade surrounds the point of attachment of the petiole) (Figure 1); the leaves of *P. arifolia* are long-petiolate and have two widely spreading basal lobes (Figure 2), whereas



FIGURE 3. Sagittate leaves of *Persicaria sagittata*. Indiana Dunes National Park, Porter County, Indiana. Photo by Michael Huft.

those of *P. sagittata* have very short petioles and are lanceolate with short and straight basal lobes that often clasp the stem (Figure 3).

Specimen Citation. MICHIGAN. Calhoun County, T3S, R4W, Sec. 1. Lat: N4214.427, Long: W08444.010. Albion. Albion College Whitehouse Nature Center. Edge successional field. Uncommon vine climbing to 2.5 m high in honeysuckle and pokeweed. [Since determined to be locally common]. *White s.n.*, Oct. 3, 2020 (ALBC, MICH, MSC).

ACKNOWLEDGMENTS

Tony Reznicek (MICH) confirmed my identification. J. Dan Skean, Jr. (ALBC) helped in the preparation of herbarium specimens. David Mindell of PlantWise LLC mapped the Whitehouse Nature Center population. Jason Raddatz, Director of the Whitehouse Nature Center, led the eradication effort there. Michael Huft provided photos of *P. arifolia* and *P. sagittata*.

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BOOK REVIEW

Jennifer Ogle, Theo Witsell, and Johnnie Gentry. *Trees, Shrubs, and Woody Vines of Arkansas*. 2021. The University of Arkansas Press. xvi + 520 pp. ISBN 978-0-912456-00-3. Paperback. \$29.95.

It might seem unusual that a woody plant book for a state as far away as Arkansas would be useful in the Great Lakes region, but, although Arkansas does have a modest Gulf Coast element in its flora, with one native palm and a few broad-leaved evergreens, it also has mountains, and widespread temperate species are well represented. The book notes that 471 species of tree, shrub, and woody vine, native and alien, are treated—not too different from the 454 species that occur in Michigan. The overlap in species is significant; about 40% of Arkansas woody plants also occur in Michigan. So it is helpful from that viewpoint. The treatments of a number of genera in this book actually cover all the species in those genera known in the Great Lakes region. At 520 pages, this book also contains much detailed information about all species that are treated in full.

The format of the book is quite straightforward. There is a detailed and well-illustrated introductory section on the Arkansas landscape and on the biogeography and ecology of the state's woody plants. Before the actual species accounts, there is a guide to what is included in each account and where in the account to find certain information. There is an illustrated glossary here, supplementing the glossary at the end of the book, with tips on plant identification that should be helpful to people starting out on the adventure of naming plants. In a section called a "visual key to genera," there is a set of pictures divided into groups (trees, shrubs, and woody vines) that illustrate distinctive features of each genus with two or more photos. This is meant to get users quickly to the right genus, and it looks quite workable.

The species treatments in the main section of the book are alphabetical by family within each of three major groups: gymnosperms, monocots, and dicots. Each family has a brief introductory paragraph, as does each genus that includes more than one species. Unlike some popular illustrated guides, this book has proper dichotomous keys for those genera with more than one species. The species treatments offer a great deal of information, including state status, fairly extensive descriptions, notes about similar species with identification tips, a color coded county level distribution map, notes on habitats and ecology, and information about wildlife and human uses and history. A particularly useful feature is the many good quality color photos illustrating different life stages as well as the major parts of the plants.

At the end of the book is a list of species of conservation concern, including some more northern species common in the Great Lakes region, and also a list of invasive woody plants, which also includes many familiar to us! Recent name

changes are noted here as well, and there is a bibliography, a list of photographers, and an index to both scientific and common names.

A number of species of woody plants native in the southern United States are cultivated in Michigan, and some of these are well known as escapes—*Robinia pseudoacacia* and *Machura pomifera* are well-known examples, but there are others, such as *Amorpha fruticosa*, *Aralia spinosa*, *Ilex opaca*, *Liquidambar styraciflua*, *Magnolia acuminata*, and more. For all of these, this book has much additional information and excellent photos.

Aliens are included, so from a Great Lakes region perspective, this means there are quite useful keys to difficult groups of aliens, like *Ligustrum*, the privets. This book may well offer insight into additional species that will be found as invaders in our area in the future. A minor criticism is that some aliens, found thus far only in a local area (often in more urban areas), are not given full treatment and are only briefly noted. Some of these are surely destined to spread, so more information about them will be needed soon enough.

Though the woody floras of Arkansas and the Great Lakes region have significant overlap, there are obviously some striking differences. Arkansas is lucky to have only one *Amelanchier*, *A. arborea*, very different from the tangles of species in the Great Lakes region. There are only six willows in Arkansas—all but one of which also occurs in the Great Lakes region—compared to 26 species in Michigan alone. Conversely Arkansas has 7 hollies, compared to three in the Great Lakes region, and a substantial 28 species of oaks, more than double the number in the Great Lakes region.

Arkansas does have a number of exciting woody plants. The mountains in Arkansas, loosely termed by people from far away as the “Ozarks,” but in reality more complex and consisting of several different ranges, are regions well known for endemic plants, though less thoroughly botanized than the Appalachians. Here occurs a rare endemic indigo shrub, *Amorpha ouachitensis*, a taller cousin to Michigan’s rare native *A. canescens* (also rare in Arkansas). Also noteworthy is a very local shrubby oak species, known from only four sites in the Arkansas mountains, *Quercus acerifolia*; as the name suggests, it is an oak with leaves that are maple-like! Perhaps most astonishing is the mysterious Stern’s Medlar, discovered in 1969 at one tiny site on the Mississippi alluvial plain. It was first described as the only American species of medlar—and the second species of the genus *Mespilus*, otherwise known only from southwestern Asia and southeastern Europe. More recently, DNA evidence has suggested that it is a *Mespilus* X *Crataegus* hybrid, remarkable in itself, as *Mespilus* is not native to North America. The hypothesis that it originated as a chance hybrid from a planting of medlars in the area long ago also seems implausible, as medlars are not commonly grown. Likely much to the dismay of botanists and naturalists in the Old World, study of this species also finally prompted the acknowledgement that *Crataegus* and *Mespilus* are not supportable as distinct genera (Lo et al. 2007).

Although it is well designed as a field guide for Arkansas, this book will also be a helpful reference for people in the Great Lakes region. But hopefully, it will also stimulate people to visit Arkansas!

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BOOK REVIEW

Paul E. Rothrock. 2021. *Sedges of Indiana and the Adjacent States, Volume II: The Carex Species*. Indiana Academy of Science, Indianapolis, Indiana. xiv + 362 pp. hardcover. ISBN 978-1-883362-16-4. \$55.00.

This volume concludes Paul Rothrock's masterful survey of the sedges (family Cyperaceae) of Indiana. The first volume, published in 2009, covered the "non-*Carex* species," 18 genera in all (Rothrock 2009). The new volume, long-awaited by sedge aficionados, field botanists, wetland and restoration ecologists, and others, is devoted to the large genus *Carex*. This follows the same format used in the first volume. For species known to occur in Indiana, each treatment includes (i) the botanical name (including naming authority) and at least one common name as well as the derivation of the botanical name, (ii) relevant synonyms, (iii) a concise description, (iv) a characterization of the habitat, (v) a list of likely associated species, (vi) a statement of the status of the species, which may include its rarity status in the state listing or limitations in its distribution in Indiana, (vii) remarks, which contain general comments providing more information about the species, and (viii) two maps—one indicating the counties in Indiana where the species has been documented and one indicating which states among Indiana and the five surrounding states (Michigan, Ohio, Kentucky, Illinois, and Indiana) the species has been recorded from. The maps are color-coded to indicate relative abundance or rarity. Intraspecific taxa are not treated separately, but are discussed, often with identification keys, in the remarks section under the relevant species.

The book is profusely illustrated with two or more photos accompanying most species accounts that show the general habit and details of the morphology. The main part of the book is organized taxonomically, starting with a description of the genus *Carex* and keys to the five subgenera and 42 sections. The subgenera, sections, and species are then treated alphabetically within each category, and descriptions and often a short discussion are provided for those subgenera and sections that have more than a single species in the six-state area covered by the book. A key to species is provided for each section with more than one species. Species that are known from one or more of the five surrounding states but not from Indiana are included in the keys, but are treated only very briefly in the alphabetical listing, including only the botanical and common names and a short statement of habitat and distribution. The keys appear to be well-constructed with couplets that are distinct and with very little or no overlap. Great pains have clearly been taken to make this book as easy as possible to use in identifying the species in this difficult group—excellent keys, brief descriptions that emphasize important identifying characters, well-chosen photographs, and information on habitat and distribution that aid in identification. Comments,

sometimes extensive, also provide aids to identification as well as additional useful information about the species.

Important and useful information is also included in the front part of the book. The introduction contains a primer on sedges, including morphology, specialized terminology, ecology, and their use in landscape design, with a special section of instructions for beginners. A guide to using the species accounts appears here, as does an explanation of the coefficient of conservatism, which appears with each species account. A special feature is the inclusion of two “guest essays” written by two of the foremost students of the genus *Carex*: an account of chromosome behavior in *Carex* and its relationship to sedge diversification by Andrew L. Hipp, and a review of how the *Carex* flora of Indiana fits into the global picture, including the origin of the genus in Asia and its subsequent evolution and dispersal by Anton A. Reznicek.

In addition to an extensive bibliography and index, the book has a glossary and five appendices, which include a checklist of all *Carex* species in Indiana along with the coefficient of conservatism and wetland status of each, changes in botanical names since Deam’s *Flora of Indiana* (Deam 1940), changes in the *Carex* flora of Indiana since 1940, a list of addenda to the earlier volume—the non-*Carex* species of Indiana—and a list of ant species associated with *Carex* species prepared by Laura Rericha, the co-author of the *Flora of the Chicago Region* (Wilhelm and Rericha 2017).

A special feature is the collection of beautiful and detailed drawings of *Carex* species and individual structures on the endpapers by the outstanding botanical artist Kathleen Marie Garness. Included with the book as extras, but not bound with it, are three glossy inserts showing a map of the glacial boundaries of Indiana, another of counties of Indiana, a map of the natural regions of Indiana, and a synopsis of Indiana *Carex* species.

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—Michael Huft